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Ecology of feral cats *Felis catus* and their prey in relation to shrubland fire regimes

Tim S. Doherty
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Ecology of feral cats *Felis catus*
and their prey in relation to
shrubland fire regimes



Tim S. Doherty

BSc (Hons) Murdoch University

Thesis submitted for the degree of Doctor of Philosophy
in the School of Natural Sciences, Faculty of Health, Engineering and Science

Edith Cowan University

June 2015

*“Let it be remembered how powerful
the influence of a single introduced tree
or mammal has been shown to be.”*

—Charles Darwin, 1859

Abstract

Invasive predators are major drivers of global biodiversity loss and their impacts may be worsened by other disturbances such as fire. I examined how the fire history of shrublands influences the ecology of feral cats *Felis catus*, dingoes *Canis dingo* and their prey species in Western Australia's northern Wheatbelt region.

A review of the literature revealed that feral cats inhabit a diverse range of ecosystems worldwide, but are generally recorded most often in habitat types characterised by a mixture of plant growth forms close to ground level. Cat habitat use is influenced by predation/competition, prey availability, shelter availability and anthropogenic resource subsidies. Relatively few studies were available for review and the strength of evidence contained within them was generally low, which highlighted the need for more rigorous field studies.

I examined overlap in resource use between cats and dingoes using remote camera surveys and dietary analysis of scats. Both carnivores were recorded in all four major habitat types: recently burnt shrublands (10 to 14 years since last fire), long unburnt shrublands (34 to ~49 years), very long unburnt shrublands (> 50 years), and woodlands. Dingoes and cats preferred woodlands and very long unburnt shrublands respectively, but spatial overlap between the two species was still common. Mean diurnal activity time for feral cats was two and a half hours later than that of dingoes. The diet of feral cats was more diverse than that of dingoes and dietary overlap between the two carnivores was relatively low. Rabbit remains did occur relatively frequently in both cat and dingo scats, but small mammals, reptiles and birds were also common in cat scats, and macropods in dingo scats.

Nine of the 15 prey species studied showed a preference for either recently burnt or long unburnt shrublands. Two small mammals and three reptiles were most abundant in recently burnt areas, while the abundance of one small mammal and three reptiles was highest in long unburnt areas. Using giving-up density experiments, I showed that rodents exhibited differential foraging behaviour in the two vegetation fire ages. The rodents foraged for longer in sheltered compared to open microhabitats, but this pattern only occurred in recently burnt, not long

unburnt shrublands, probably because the higher density of understorey vegetation in recently burnt areas provided the rodents with extra cover to hide and escape from predators.

I also developed a new framework for conceptualising interactions between invasive predators and other ecological disturbances, such as fire, habitat fragmentation, and top-predator decline. The impacts of invasive predators can be classified as either functional (density-independent) or numerical (density-dependent), and they interact with other threats through both habitat-mediated (fire, grazing, land clearing) and community-mediated (top-predator decline, altered prey populations, anthropogenic resource subsidies) interaction pathways.

The key findings of this thesis show that both old and young shrublands can be suitable habitat for feral cats; predator-prey dynamics are influenced by successional habitat stages; small mammals show behavioural, as well as population-level responses to fire; and that invasive predator management is likely to benefit from addressing multiple threats in unison.

The declaration page
is not included in this version of the thesis

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Dr Dale Nimmo

Russell Palmer

Dr Euan Ritchie

Dr Sue Robinson

Dr Eddie van Etten

The research described in this thesis was my original idea, I led the development of the questions and hypotheses at all stages, undertook the fieldwork and analyses, and completed the writing. The above list of co-authors contributed in one or more of the following ways to the thesis components published in journals: data collection, provision of unpublished datasets, analyses, or development and editing of manuscripts. I was the lead author in all cases and my contributions are detailed at the end of the thesis in the *Co-author statements* section.

Publications arising from this research

The thesis is presented in the 'thesis with publications' format. Chapters 2, 4, 5 and Appendices A and D are presented as reformatted copies of the published articles; hence there is some repetition of site descriptions and methodology throughout. The acknowledgements, but not the abstracts, have been reproduced for each paper, although I present a single reference list for the entire thesis. The original abstracts can be found in the '*Copies of original publications*' section. Chapters 1, 3 and 6 contain material adapted from published papers of which I am the lead author. I warrant that I have obtained, where necessary, permission to use in this thesis any of my own published work in which the copyright is held by another party.

Chapters 1 and 6 (partial):

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Chapter 2:

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Appendix A:

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Table of Contents

Abstract.....	iii
Declaration	v
Acknowledgements	vi
Statement of contribution of others.....	viii
Publications arising from this research.....	ix
Table of Contents.....	x
List of Figures.....	xii
List of Tables.....	xvi
Chapter 1. General introduction and study site description.....	1
History and impacts of cats in Australia.....	3
Influence of fire on predator-prey dynamics	5
Interactions between predators	6
Study rationale and aims.....	7
Study site description.....	8
Chapter 2. A critical review of habitat use by feral cats and key directions for future research and management	12
Introduction.....	12
Methods	14
Results	16
Discussion.....	21
Acknowledgements	29
Chapter 3. Overlap in the diet and habitat use of feral cats and dingoes at a semi-arid rangeland site.....	30
Introduction.....	30
Methods	32
Results	43
Discussion	51
Acknowledgements	57
Chapter 4. Response of a shrubland mammal and reptile community to a history of landscape-scale wildfire	58
Preface.....	58
Introduction.....	58
Methods	60
Results	66
Discussion.....	71
Acknowledgements	75
Supplementary material.....	76
Chapter 5. A game of cat-and-mouse: microhabitat influences rodent foraging in recently burnt, but not long unburnt shrublands	79
Introduction.....	79
Materials and Methods.....	81
Results	87
Discussion	90
Acknowledgements	93

Chapter 6. Synthesis and conclusions	94
Summary of major findings.....	94
Synthesis	98
New conceptual framework.....	101
Concluding remarks	105
Appendix A. A continental-scale analysis of feral cat diet in Australia	106
Introduction.....	106
Materials and methods.....	108
Results	112
Discussion	119
Acknowledgements	124
Supplementary materials.....	124
Appendix B. Supplementary materials for Appendix A	125
Appendix C. GPS collaring of feral cats	138
Introduction.....	138
Methods	138
Results and Discussion.....	141
Appendix D. Response of feral cats to a track-based baiting programme using <i>Eradicat</i>[®] baits	147
Introduction.....	147
Methods	149
Results	154
Discussion	157
Acknowledgements	159
References	160
Co-author statements	185
Copies of original publications	191

List of Figures

Figure 1.1 A: Location of the study area in south-western Australia; B: Location of the study area in the Avon Wheatbelt bioregion (AVW); C: Property boundaries and distribution of vegetation fire ages. NB: not all minor roads and tracks are shown. White areas on the map have no known fire age and are considered to have remained unburnt for 50–100+ years ('very long unburnt'). Bioregions in map B: GES, Geraldton Sandplains; YAL, Yalgoo; MUR, Murchison; COO, Coolgardie; JAF, Jarrah Forest; SWA, Swan Coastal Plain.....	9
Figure 1.2 Changes in shrubland structure with increasing time since fire. Clipart images are sourced from the Integration and Application Network (www.ian.umces.edu/symbols/). NB: Due to spatial and temporal variation in sampling strategies, some parts of the thesis refer to 'recently burnt' vegetation as being 10–13/14 years old.	11
Figure 2.1 World map showing the locations of the reviewed studies on habitat use by feral and unowned cats (<i>Felis catus</i>). Numbers refer to studies listed in Table 2.1.....	15
Figure 2.2 Frequency of studies where cats favoured (grey bars with + symbol) or avoided (white bars with – symbol) seven broad habitat components: forest, woodland, grassland, shrub/heathland, riparian areas, agricultural land, and infrastructure.....	17
Figure 2.3 Frequency of studies suggesting factors that may explain observed patterns in cat habitat use: Level 1 (solid white); Level 2 (solid grey); Level 3 (diagonal stripe); Level 5 (solid black). No studies were classed as Level 4.	18
Figure 2.4 Conceptual model to describe factors that can potentially influence habitat use by feral cats. Ecosystem components that influence habitat use are hierarchical (A), i.e. predators have a stronger influence than prey, but prey increases in importance where predators are absent. Habitat choices are behaviourally stratified (B) and broad habitat components that cats favour (+) or avoid (–) are nested in the landscape (C). Studies that provide support for or inferences regarding each component are listed using subscripts that correspond to study numbers in Table 2.1.....	26
Figure 3.1 Location of the study area in Western Australia's northern Wheatbelt. The area nested within Mt Gibson Wildlife Sanctuary is managed for mining. UCL, Unallocated Crown Land.	32
Figure 3.2 Distribution of habitat types and location of the remote cameras and sand pad transects. The locations of cameras N5, N19 and N20 are not shown on the map because they were excluded from analyses.....	34
Figure 3.3 Cumulative diversity (H_k) of cat (dashed line) and dingo (solid line) diet with increasing sample size of scats.....	44
Figure 3.4 Frequency of occurrence (% <i>F</i>) and volume occurrence (% <i>V</i>) of food groups in feral cat and dingo scats.	44
Figure 3.5 Spatial intensity of feral cat, dingo and rabbit activity. Darker circles represent higher activity, and white circles represent sites where cats, dingoes or rabbits were never recorded. Cat and dingo AI: number of photos per 100 camera-nights for the entire study	

period, excluding May 2014. Rabbit activity: number of plots with rabbit activity per 100 nights.....	46
Figure 3.6 Frequency of photo events during each hour of the day and night for feral cats and dingoes. The black arrows indicate approximate mean activity time.	47
Figure 3.7 Means and standard errors of small mammal, reptile and total abundance in three habitat types: recently burnt shrublands, long unburnt shrublands and woodlands.	50
Figure 4.1 Location of recently burnt sites (black symbols) and long unburnt sites (white symbols) in the study area. Group 1 sites are triangles and Group 2 sites are circles. Grey shaded areas were aged 8–13 years since last fire at time of sampling ('recently burnt') and the remaining area was mostly long unburnt (25–50 years) or very long unburnt (> 50 years).	61
Figure 4.2 Mean abundance per 100 nights and standard error bars for recently burnt and long unburnt habitat. *statistically significant difference. C.mac, <i>Ctenophorus maculatus</i> ; C.scu, <i>Ctenophorus scutulatus</i> ; C.mim, <i>Ctenopus mimetes</i> ; C.pan, <i>Ctenopus pantherinus</i> ; D.gra, <i>Diplodactylus granariensis</i> ; L.ino, <i>Liopholis inornata</i> ; L.mai, <i>Lucasium maini</i> ; M.gre, <i>Menetia greyii</i> ; N.mit, <i>Notomys mitchellii</i> ; P.her, <i>Pseudomys hermannsburgensis</i> ; S.cra, <i>Sminthopsis crassicaudata</i> ; S.dol, <i>Sminthopsis dolichura</i> ; S.gil, <i>Sminthopsis gilberti</i> ; C.scho, <i>Ctenopus schomburgkii</i> ; D.pul, <i>Diplodactylus pulcher</i>	68
Figure 4.3 Significant mixed modelling relationships between species abundance and microhabitat variables. Recently burnt sites are solid black circles and long unburnt sites are white circles with a black outline. The solid black line is the fitted model and the shaded area is the 95% confidence band.....	70
Figure 4.4 Plots of residual and fitted values for linear mixed models to test the effect of vegetation fire age on fauna species abundance. The error distribution used in each model is listed in Table 4.2 in the main document.	76
Figure 5.1 Location of recently burnt (black circles) and long unburnt (white circles) giving-up density experiment sites. Additional sites where pitfall trapping was undertaken are shown with square symbols. Small gray diamonds represent the location of remote cameras. The gray shading represents the distribution of shrublands that were last burnt 9–13 years prior to sampling, and most other areas were unburnt for > 40 years.....	82
Figure 5.2 Plots of mean GUD values and SE bars for the effects of fire history and microhabitat on the 'mouse group' (upper panel; <i>Pseudomys hermannsburgensis</i> and <i>Mus musculus</i>) and <i>Notomys mitchellii</i> (lower panel) foraging activity. Sample sizes are in parentheses. GUD, giving-up density.	88
Figure 5.3 Mean and SE bars for the abundance of <i>Notomys mitchellii</i> , <i>Pseudomys hermannsburgensis</i> , and <i>Mus musculus</i> in spring (October) 2012 and autumn (April) 2013.	88
Figure 6.1 Conceptual model of the relationship between community- and habitat-mediated interaction pathways and their effects on native fauna. Habitat-mediated pathways are processes that modify the structure or integrity of habitat and in turn exacerbate the	

impacts of invasive predators (A) on native fauna (B). Community-mediated interaction pathways are changes in the presence or abundance of a top-predator or its prey species that can lead to increased population densities or altered behaviour of invasive predators that in turn exacerbate their impacts on native fauna. The primary threats interacting with invasive predators are: (1) land clearing; (2) grazing; (3) fire; (4) top-predator decline; (5) altered prey populations; and (6) anthropogenic resource subsidies. Additional processes are indicated with italicised text. Solid lines represent positive effects (+) and dashed lines represent negative effects (-). Image credits: 1, endymion120 (Flickr, CC BY 2.0); 2, USDA (public domain); 3 & 5, CSIRO (CC BY 3.0); 4, 6, A & B, T. Doherty..... 102

Figure A.1 Study locations and climate-habitat regions. ARID, deserts and xeric shrublands; EAST, eastern inland shrub/grass/woodlands and savannas; I, islands; SE, south-east temperate forests and heath; SW, south-west shrublands, woodlands and forests; TROP, tropical grasslands, savannas, shrublands and forests. 110

Figure A.2 The frequency of occurrence (FO) of feral cat food groups in Australia modelled as a function of environmental and geographical predictors: (a-d) latitude with arthropod, rabbit, rodent and reptile FOs; (e) longitude with medium-sized mammal FO; (f-h) mean annual temperature ($^{\circ}\text{C} \times 10$) with reptile, rodent and rabbit FOs; (i-k) mean annual precipitation (mm) with arthropod, reptile and medium-sized mammal FOs; and (l-n) environmental productivity (NDVI) with reptile, arthropod and medium-sized mammal FOs. The solid black line is the fitted model mean and the shaded area represents the 95% confidence intervals of the predicted mean..... 116

Figure A.3 Mean regional frequency of occurrence for (a) rabbits, rodents, dasyurids and medium-sized mammals and (b) arthropods, reptiles, birds, carrion and trophic diversity of feral cats in Australia. Trophic diversity has been standardized on a scale of 0 to 1. Error bars are bootstrapped 95% confidence intervals. ARID, deserts and xeric shrublands; EAST, eastern inland shrub/grass/woodlands and savannas; ISL, islands; SE, south-east temperate forests and heath; SW, south-west shrublands, woodlands and forests; TROP, tropical grasslands, savannas, shrublands and forests. 118

Figure A.4 Generalized additive mixed model relationships for: (a-c) trophic diversity of feral cats in Australia and frequency of occurrence (FO) of arthropods, rodents and reptiles; (d) trophic diversity and mean annual temperature ($^{\circ}\text{C} \times 10$); and (e-f) rabbit FO with rodent and dasyurid FOs. The solid black line is the fitted model mean and the shaded area represents the 95% confidence intervals of the predicted mean..... 119

Figure C.1 Trap sites and capture locations of feral cats at Charles Darwin Reserve in March 2013. 142

Figure C.2 Location of search areas covered by light aircraft and ground vehicle..... 143

Figure D.1 Location of the baited part of the reserve (grey shaded tracks) and the 40 remote camera locations (black diamonds). 150

Figure D.2 Mean cat activity (number of photographs per 100 nights) and standard error bars in the unbaited control (solid line and triangles) and baited treatment (dashed line and circles)

areas during six sampling periods. The dashed vertical lines indicate the timing of baiting in September 2013 and May 2014. 155

Figure D.3 Response of cat activity (number of photographs per 100 nights) to time (before/after) and treatment (baited/unbaited) in (a) September 2013 and (b) May 2014. Standard error bars are shown..... 155

List of Tables

Table 2.1 Summary information for the 27 studies reviewed here on habitat use by feral and unowned cats <i>Felis catus</i>	19
Table 2.2 Key directions for future research and management that aims to understand and ameliorate the impact of feral cats.....	27
Table 3.1 Survey periods for remote cameras, pitfall trapping and sand pad monitoring. Grey boxes indicate monitoring periods for which the data was excluded from the analyses in this chapter.....	35
Table 3.2 Descriptions of land systems and fire ages that were used to calculate habitat diversity at each camera site. Land systems information is based on Payne et al. (1997). Land systems that were not directly surveyed by the remote camera surveys are marked with an asterisk.	37
Table 3.3 Percentage of photo events for cats and dingoes within time brackets between successive photos on the same camera within each session	40
Table 3.4 Occurrence of prey species and food groups in feral cat, dingo and fox scats. % <i>F</i> , percentage frequency of occurrence; % <i>V</i> , percentage occurrence by volume.	45
Table 3.5 Mixed modelling results for the effect of habitat variables on cat and dingo activity, and dingo activity on cat activity. * significant at 0.05	48
Table 3.6 Habitat selection ratios (w_i) for cats and dingoes across all sessions, and cats in individual sessions. Values > 1 indicate preference for a habitat type, and values < 1 indicate avoidance. Significance (*) was inferred using a Bonferroni level of $P < 0.0125$	49
Table 4.1 Summary of trapping sites indicating number of years since last fire at time of sampling and number of nights that traps were open during each trapping period.....	63
Table 4.2 Parameter estimates and 90% confidence intervals from the fitted models for the effect of vegetation fire history on species abundance. ‘Recently burnt’ was used as the reference level in the fixed effect. ‘Significant’ fire effects were inferred where the confidence intervals of the ‘long unburnt’ estimate did not overlap zero. Significant relationships are indicated with a *	67
Table 4.3 Parameter estimates and 95% confidence intervals for microhabitat models that were well supported. Significant relationships are indicated with a *. Complete modelling results are given in Table 4.5 in Supplementary material p78	69
Table 4.4 List of reptile and mammal species captured during monitoring at Charles Darwin Reserve, Western Australia in 2010–2013.....	77
Table 4.5 Mixed model rankings (ΔAIC_c) and weights for relationships between fauna species abundance and microhabitat variables. Models with a $\Delta AIC_c < 2$ and a weight > 0.2 were explored further and are indicated here with bold text and grey shading.....	78
Table 5.1 Mean giving-up densities (number of peanuts remaining) in each combination of microhabitat and fire history treatments. Standard errors are in parentheses.....	87
Table 5.2 Parameter estimates and 95% <i>CI</i> s for the fixed effects of fire history, microhabitat, and the interaction term on proportional giving-up densities, and the variance estimates for	

random effects of sampling period and tray. Significant effects (*) were inferred where <i>CIs</i> did not overlap zero. The intercept is the contrast level in the model.....	87
Table 5.3 Mean vegetation density (number of touches in each stratum) and percent cover for recently burnt and long unburnt sites and univariate analysis of variance tests for the effect of fire history. Mean variables are untransformed. Significance level is 0.05.....	89
Table A.1 Threatened animal species consumed or killed by feral cats in Australia and their IUCN Red List status. See Table B.3 for a complete list of vertebrate species and invertebrate groups recorded as being consumed or killed by feral cats in Australia and its territorial islands.....	113
Table A.2 Generalized additive mixed modelling (GAMM) results for the relationship between environmental and geographical variables, food groups (FO) and trophic (dietary) diversity (D) of feral cats in Australia.....	115
Table A.3 Pairwise regional differences in feral cat diet composition in Australia (FO, logit-transformed; and trophic diversity, log-transformed) based on multivariate linear models.	117
Table B.1 Bibliography of published studies that contain data on the diet of feral cats <i>Felis catus</i> in Australia. Bold text indicates a study that was included in our analyses.....	125
Table B.2 Summary of the data sets used in analyses, with first author of publication or author of unpublished data set. Refer to Table B.1 for full references.....	129
Table B.3 List of vertebrate species and invertebrate groups recorded as being consumed or killed by feral cats in Australia and its territorial islands and their IUCN Red List Conservation status. * introduced species; ^ cat predation inferred as cause of mortality; CR, critically endangered; EN, endangered; VU, vulnerable; NT, near threatened; DD, data deficient (IUCN, 2013); *** the European rabbit (<i>Oryctolagus cuniculus</i>) is classed as 'near threatened' in its native range, but is an introduced pest in Australia.	131
Table C.1 Summary of capture and tracking efforts for feral cats.....	140
Table C.2 Summary of feral cats that were captured during the March 2013 trapping exercise at Charles Darwin Reserve.....	141
Table D.1 Dates of remote camera monitoring sessions and baiting events.....	152
Table D.2 Percentage of feral cat photo events in time periods for the number of minutes between successive photos on the same camera within each session.....	153
Table D.3 Mixed modelling results for the effect of time, treatment and the interaction term on cat activity at the September 2013 and May 2014 baiting events. Significant terms are indicated with bold text.	156
Table D.4 Mean cat activity (number of photographs per 100 nights) in the baited treatment area and unbaited control area before and after baiting in September 2013 and May 2014. Standard errors are given in parentheses.	156
Table D.5 Percentage of remote cameras in the baited treatment area and unbaited control area that detected feral cats before and after baiting in September 2013 and May 2014. Raw number of cameras is given in parentheses.....	156

Chapter 1.

General introduction and study site description

Invasive mammalian predators are a major driver of biodiversity loss in ecosystems across the globe. Nine of these species feature in the list of *100 of the World's Worst Invasive Alien Species* (Lowe et al. 2000), in addition to a further 21 introduced mammals that are known or potential predators of native fauna (IUCN 2014). These mammals range from obligate carnivores (e.g. *Felis catus*) to opportunistic predators (e.g. *Rattus* spp.). Three of these taxa have had a disproportionate impact on global biodiversity: the domestic cat *Felis catus*, the red fox *Vulpes vulpes* and some rats *Rattus* spp. The domestic cat on islands has contributed to at least 14% of bird, mammal and reptile extinctions globally (Medina et al. 2011) and, along with the red fox, has also contributed to the extinction of more than 20 mammal species in Australia (Woinarski et al. 2015). *Rattus rattus* is the most damaging species of rat and has contributed to the decline or extinction of 60 vertebrate species worldwide (Towns et al. 2006). In addition to predation, invasive predators can also have a number of indirect impacts on ecosystem function, potentially resulting in trophic cascades and ecosystem collapse (Croll 2005; Johnson et al. 2007; Fey et al. 2009). These impacts include resource competition (Glen & Dickman 2008), disease transmission (Banks & Hughes 2012), hybridisation (Daniels et al. 2001), and facilitation with other invasive species (Courchamp et al. 2000).

Reducing the impacts of invasive predators is a priority for conservation managers in Europe (Daniels et al. 2001; Zuberogitia et al. 2010), North America (Loss et al. 2013), the Caribbean (Coblentz & Coblentz 1985), Australia (Saunders et al. 2010; Woinarski et al. 2015), New Zealand (Lettink et al. 2010; Russell et al. 2015), and many islands (Hess et al. 2009; Ratcliffe et al. 2010; Phillips et al. 2011; Oppel et al. 2014). To date, management of the threats posed by invasive predators has focused largely on directly manipulating their populations using lethal control. The main methods include combining exclusion fencing and lethal control to create

predator-free areas (Young et al. 2013); culling, often financed using bounty systems (Bonesi et al. 2007); and poisoning, using large-scale baiting programmes (e.g. 1080 poison baiting) (Robley et al. 2014). A consistent feature of these methods is their sole focus on removing individuals to reduce or eliminate predation pressure on native prey. While these programmes have at times been successful in limiting the effects of invasive predators on prey at local scales or on islands (Whitworth et al. 2013; Robley et al. 2014), they are extremely costly (Zuberogitia et al. 2010), they have not arrested the ongoing declines of native fauna in most regions (e.g. Woinarski et al. 2015), and their applicability at larger spatial scales is questionable (Lieury et al. 2015). Further, such management programmes often occur without considering how the predators might interact with other stressors impacting ecosystems at the same time. This has led to unpredictable outcomes of invasive predator control; sometimes it is ineffectual (Bodey et al. 2011; Lazenby et al. 2014), or worse, results in a net negative outcome for biodiversity (Norbury et al. 2013; Marlow et al. 2015). These examples are supported by a rapidly growing body of evidence showing that threatening processes frequently interact to influence vulnerable species and ecosystems (Didham et al. 2007; Brook et al. 2008; Mantyka-Pringle et al. 2011; Norbury et al. 2013; Stireman et al. 2014). Processes such as habitat fragmentation, fire, and top-predator declines can interact with invasive predators to exacerbate extinction risk for native species (Crooks & Soulé 1999; Norbury et al. 2013; McGregor et al. 2014), which suggests that integrated approaches that address multiple threats in unison are likely to be most effective (Dickman et al. 2010a; Evans et al. 2011).¹

Australia provides a useful model for evaluating the complex issues around the impacts of invasive predators and other ecological disturbances. Historical and contemporary declines in Australia's mammal fauna have been attributed to interactions between multiple threatening processes (Smith & Quin 1996;

¹These first two paragraphs are adapted from the following paper of which I am the lead author: Doherty TS, CR Dickman, DG Nimmo and EG Ritchie (2015) *Multiple threats, or multiplying the threats? Interactions between invasive predators and other ecological disturbances*. *Biological Conservation*, 190:60–68.

Woinarski et al. 2011; Ziembicki et al. 2015), with Australia having the world's worst mammal extinction record—30 extinctions in total—accounting for 11% of the continent's endemic land mammals and 35% of mammal extinctions globally (Woinarski et al. 2015). Two invasive predators are the primary agents of these declines, with feral cats and red foxes contributing to 22 and 13 mammal extinctions respectively, and the decline of many other species (Woinarski et al. 2015). Most of these species are arid-zone, ground-dwelling taxa with a body mass between 35 and 5,500 g—traits that make them particularly vulnerable to predation by cats and foxes (Burbidge & McKenzie 1989; Johnson & Isaac 2009). The extinctions began around 1840—just 50 years after European settlement—and then continued through the 20th century up until the present day (Johnson 2006; Woinarski et al. 2015). Other major threatening processes that have contributed to this extreme rate of extinction include habitat loss and fragmentation, habitat alteration by livestock and feral herbivores, altered fire regimes, and disease (Johnson 2006; Woinarski et al. 2015). From herein, I focus on the impacts and management of feral cats, rather than foxes, because of the challenges inherent in managing cats (Fisher et al. 2014b), a history of effective fox control (Saunders et al. 2010), and strong evidence that cats are driving a new wave of mammal declines in Australia (Ziembicki et al. 2015).

History and impacts of cats in Australia

The earliest known introduction of domestic cats to Australia was by European settlers at multiple coastal locations during the period 1824–86 (Abbott 2002). Cats were initially kept as companion animals and pest control agents in settlements and on farms, but they inadvertently dispersed into the natural environment and formed self-sustaining feral populations (Rolls 1969; Abbott 2002). With the expansion of European settlements, cats spread rapidly and had colonised 90% of the continent by the 1890s (Abbott 2002). Their success was in part aided by the release and spread of European rabbits *Oryctolagus cuniculus*, which provided a stable and abundant food source across much of the continent (Rolls 1969; Abbott 2008). At times, cats were even transported to and intentionally released at locations where rabbit plagues were a major problem (Rolls 1969; Abbott 2008).

Feral cats live and reproduce in the wild, survive by hunting or scavenging, and have no direct dependence on humans. Being a generalist, obligate carnivore, the feral cat feeds mainly on small and medium-sized mammals, such as rodents and rabbits (Fitzgerald & Turner 2000), although in Australia its diet also includes lizards, snakes, frogs, marine and terrestrial bird species, arboreal and ground-dwelling marsupials, and carrion (Appendix A). Although there is no unequivocal evidence implicating cats as the sole extinction agent for Australian mammals, statistical modelling has revealed temporal and spatial relationships between the arrival or presence of cats in an area and the decline of native mammals (Burbidge & McKenzie 1989; Smith & Quin 1996; McKenzie et al. 2007). Smith and Quin (1996) identified cats as the primary driver of decline for small (10–35 g) conilurine rodents (Conilurini), and for conilurine rodents of all sizes in areas where rabbits and foxes are scarce or absent. Also, Burbidge and Manly (2002) found that both cats and foxes were associated with mammal extinctions on Australian islands and the effect of cats was worst on arid islands. Further evidence for their impacts has been drawn from molecular analysis of predation events (Glen et al. 2009; Marlow et al. 2015) and the relative persistence or failure of reintroduced mammal populations inside or outside of predator-proof reserves and islands (Short & Turner 2000; Moseby et al. 2011b).

There have only been a few experimental studies of feral cat impacts in Australia. At Shark Bay in Western Australia, capture rates of small mammals declined by 80% in a low fox density and high cat density treatment, while capture rates doubled in a low fox and low cat treatment (Risbey et al. 2000). The control area with moderate cat and fox densities maintained intermediate numbers of small mammals (Risbey et al. 2000). At the Arid Recovery reserve in South Australia, rodent abundance in a fenced reserve where cats, foxes and rabbits had been eradicated was 15 times higher than outside the reserve (Moseby et al. 2009a). Finally, in the Northern Territory, feral cats quickly extirpated reintroduced populations of long-haired rats *Rattus villosissimus* in two predator-accessible areas, while two predator-proof populations persisted (Frank et al. 2014). Taken together, these results confirm that feral cats can suppress and exterminate populations of small mammals. Cats may also impact native fauna through resource competition (Glen & Dickman 2008; Pavey et al. 2008) and

transmission of the protozoan parasite *Toxoplasma gondii* (Canfield et al. 1990; Bettiol et al. 2000), although empirical evidence of these effects is lacking (but see Fancourt et al. 2014).

Influence of fire on predator-prey dynamics

Fire causes dramatic changes in vegetation structure and hence has strong effects on plant and animal communities, particularly in fire-prone regions. These effects include animal mortality (Hailey 2000; Smith et al. 2012b) and changes in food availability (Vernes et al. 2004; Valentine et al. 2014), resource competition (Sutherland & Dickman 1999) and nesting resources (Saab et al. 2007), ultimately leading to changes in habitat suitability and associated shifts in community composition (Horn et al. 2012; Nimmo et al. 2012a). Although fire is a natural disturbance, anthropogenic pressures have altered fire frequency, intensity and size in many parts of the world (Penman et al. 2011), hence many animal species are threatened by altered fire regimes that change habitat or resource availability beyond natural perturbations (e.g. Ager et al. 2007; Valentine et al. 2011).

Predator-prey systems present an interesting case study when it comes to the influence of fire-induced habitat changes on animal communities. Predation risk is generally lower in sheltered compared to open habitats (Verdolin 2006; Janssen et al. 2007), hence the loss of vegetation cover following fire can result in higher predation rates of small mammals in burnt compared to unburnt areas (Conner et al. 2011; Leahy 2013). Declines in the survival, abundance and rates of transition to reproductive states of hispid cotton rats *Sigmodon hispidus* following prescribed fire were attributed to increased rates of predation (Morris et al. 2011). Predators are often attracted to recently burnt areas because of the improved hunting opportunities these areas provide (Dees et al. 2001; Birtsas et al. 2012; McGregor et al. 2014). Birtsas et al. (2012) found that visitation rates of foxes and dogs *Canis lupus familiaris* at sampling stations in an intensely burned area were greater than in both a moderately burned area and an unburned area, and McGregor *et al.* (2014) found that feral cats in northern Australia preferentially hunted in areas that had recently been grazed or intensely burnt. This suggests that early post-fire habitats can be particularly risky environments for prey species.

Although largely untested, the loss of vegetation cover following fire is also likely to cause changes in prey species behaviour (Stokes et al. 2004; Spencer et al. 2005). For example, experimental reduction of vegetation cover on Australia's Fraser Island led to changes in the foraging behaviour, abundance and size structure of bush rat *Rattus fuscipes* populations (Spencer et al. 2005). Bush rats spent less time foraging in areas where cover had been reduced, probably because of an increase in perceived predation risk (Spencer et al. 2005). Consequently, the combined effects of fire and predation are likely to have considerable impacts on prey populations (Morris et al. 2011; Leahy 2013), and may be worse still when the predator is an introduced species (Salo et al. 2007). Recent evidence from northern Australia supports this notion, where the impacts of feral cats are exacerbated by changes in fire and grazing regimes, leading to severe declines of native mammal populations (Woinarski et al. 2011; Leahy 2013; McGregor et al. 2014; Ziemnicki et al. 2015). Because fire is a major part of many Australian ecosystems (Russell-Smith et al. 2007; Murphy et al. 2013) and its incidence is predicted to increase with future climatic changes (Williams et al. 2001; Pitman et al. 2007), understanding the combined effects of fire and predation is essential to preventing further extinctions.

Interactions between predators

Predation and competition from sympatric predators may also play a role in moderating the impacts of feral cats. Cats are often recorded less frequently at sites where larger carnivores are common, including dingoes *Canis dingo* (Brook et al. 2012), Tasmanian devils *Sarcophilus harrisi* (Lazenby & Dickman 2013), coyotes *Canis latrans* (Gehrt et al. 2013), red foxes (Molsher 1999) and dogs *Canis lupus familiaris* (Krauze-Gryz et al. 2012). The mechanism driving these patterns may be interference competition (e.g. aggressive encounters) and/or exploitation competition (e.g. use of a shared resource) (Polis et al. 1989). Documenting the degree of overlap in resource use is a useful first step in determining whether resource competition may exist between sympatric carnivores.

Feral cats are sympatric with native dingoes and introduced foxes in many parts of Australia and moderate to high levels of dietary overlap between the three carnivores suggest strong potential for exploitation competition (Glen & Dickman

2005). Additional observations confirm that dingoes will kill and/or consume foxes and cats (Marsack & Campbell 1990; Moseby et al. 2012), and the same for foxes to cats (Molsher 1999; Paltridge 2002). There is a growing body of knowledge showing that both dingoes and foxes can have temporally and spatially suppressive effects on cat habitat use, activity or abundance (Molsher 1999; Risbey et al. 2000; Brawata & Neeman 2011; Brook et al. 2012; Wang & Fisher 2013; Marlow et al. 2015). Brook et al. (2012) found that cat activity was higher and that cats were active earlier in the night at sites where dingoes were subject to lethal control compared to sites without lethal control. Wang and Fisher (2013) also found evidence of temporal segregation between cats and dingoes. These observations suggest that an understanding of how invasive mesopredators interact with intra-guild species is necessary if their impacts are to be reduced.

Study rationale and aims

Given the major role of feral cats in Australia's mammal extinctions and strong potential for fire regimes and sympatric predators to influence their impacts, an integrated understanding of the relative importance of these factors and potential synergies between them is required if the impacts of feral cats are to be reduced. In this thesis, I use a combination of review and field studies to investigate the influence of shrubland fire regimes on feral cats, their prey species and competitors (dingoes) in south-western Australia. Foxes are not examined in detail because they were uncommon at the study site. The thesis is structured around five key objectives:

- Objective 1: Critically review the literature to identify the primary factors influencing feral cat habitat use (Chapter 2);*
- Objective 2: Examine habitat selection by cats with regard to the fire history of vegetation and the factors driving this (Chapter 3);*
- Objective 3: Investigate overlap in resource use between sympatric cats and dingoes (Chapter 3);*
- Objective 4: Identify patterns of prey habitat selection to assess whether some species are at a greater risk of predation due to habitat selection by cats (Chapter 4); and*
- Objective 5: Determine whether fire-induced changes in habitat structure influence the behaviour of cat prey species (Chapter 5).*

In the final chapter, I integrate the findings of the four main chapters into a broad understanding of the role of fire in predator-prey dynamics and how this information can inform management of invasive predators. To this end, I also present a new framework for conceptualising interactions between invasive predators and other ecological disturbances.

The original primary aim of this thesis was to investigate cat habitat selection, movements and other aspects of their spatial ecology using GPS tracking collars. Although I fitted GPS collars to a sample of cats, apparent equipment failure and other possible factors prevented any data from being retrieved. I detail this in Appendix C to provide context to Chapter 3. The resultant thesis objectives are broadly similar to the original objectives, although I was unable to examine fine-scale habitat selection by cats, nor their home range sizes. I also present a quantitative analysis of feral cat diet in Australia (Appendix A), and detail the results of a poison baiting trial that was conducted at the study site during the study period (Appendix D).

Study site description

The study site for this work was Charles Darwin Reserve (CDR), a 68,000 ha pastoral lease 350 km north-east of Perth in Western Australia's northern Wheatbelt region (29° 35' S, 116° 58' E; Figure 1.1). The reserve is managed for conservation by Bush Heritage Australia (BHA) and was de-stocked of sheep and goats in 2003. Surrounding land includes Wanarra station to the west, the destocked Mt Gibson Wildlife Sanctuary to the east, the partially destocked Ninghan station to the north-east and Unallocated Crown Land to the south (Figure 1.1). The 1,170 km State Barrier Fence, which was built to exclude dingoes from agricultural land in the southwest of the state, runs through the study area. The climate is semi-arid Mediterranean, with cool winters, hot summers and low rainfall (mean 306 mm year⁻¹ at the adjacent Wanarra pastoral station; Bureau of Meteorology 2014).

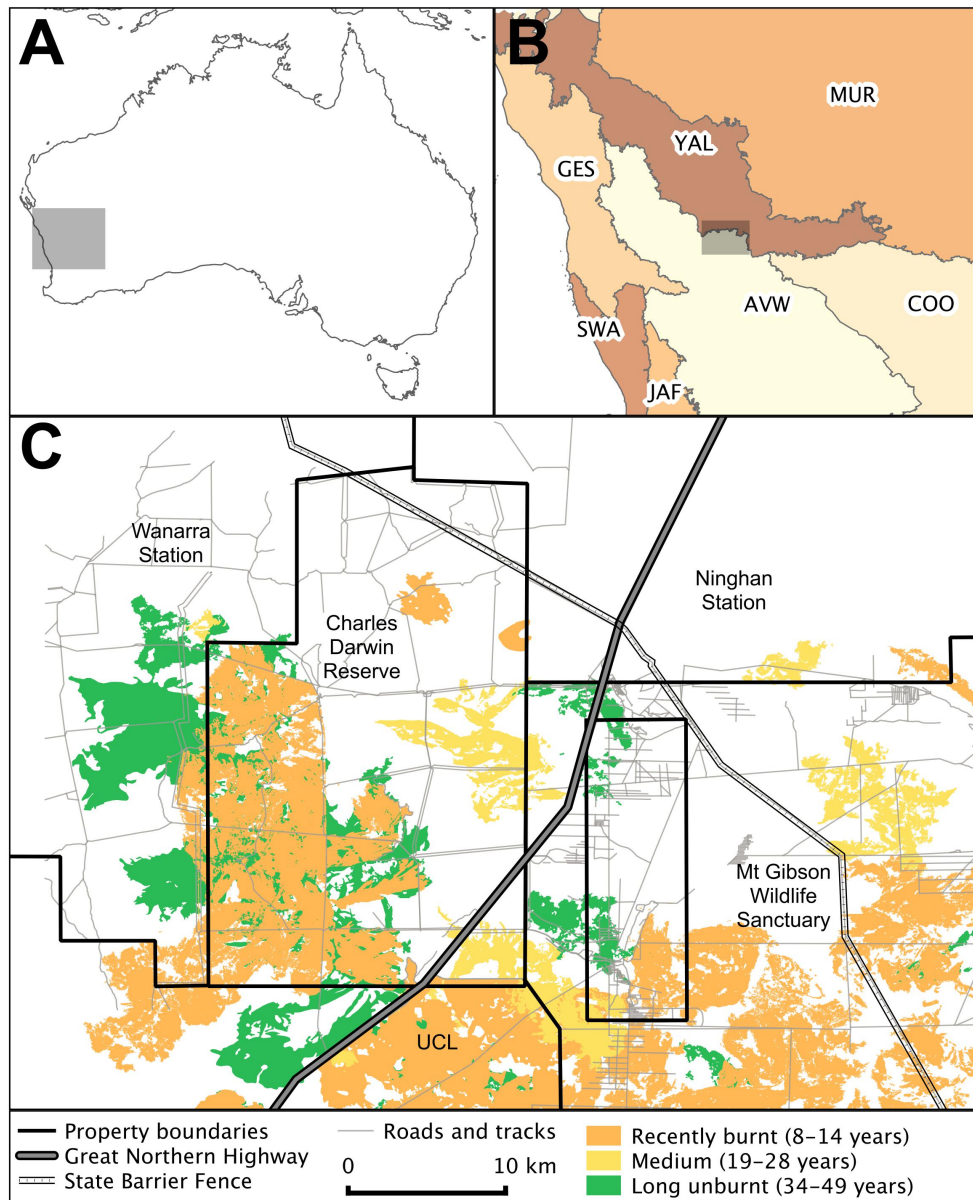


Figure 1.1 A: Location of the study area in south-western Australia; B: Location of the study area in the Avon Wheatbelt bioregion (AVW); C: Property boundaries and distribution of vegetation fire ages. NB: not all minor roads and tracks are shown. White areas on the map have no known fire age and are considered to have remained unburnt for 50–100+ years ('very long unburnt'). Bioregions in map B: GES, Geraldton Sandplains; YAL, Yalgoo; MUR, Murchison; COO, Coolgardie; JAF, Jarrah Forest; SWA, Swan Coastal Plain.

Vegetation

The reserve lies within the Avon Wheatbelt P1 bioregion, of which > 80% has been cleared of its native vegetation since European settlement (Department of Agriculture and Food WA 2007). The reserve contains 716 plant taxa, including 29 threatened plant species (BHA, *unpublished data*). The major vegetation types within the broader study area are: shrublands, *Eucalyptus salubris* woodlands, *Eucalyptus loxophleba* woodlands, greenstone hills and ironstone ranges, and seasonal salt lakes (Payne et al. 1997). Around half of the reserve's area is comprised of dense mixed-species shrublands on deep yellow sands (the 'Joseph' land system *sensu* Payne et al. 1997) and the remainder is a mixture of eucalypt woodlands and other vegetation types (Braun 2006). The shrublands are dominated by *Acacia* species, but also contain other shrub genera like *Allocasuarina*, *Melaleuca*, *Hakea* and *Grevillea*.

A history of unplanned fire at CDR has resulted in around 69% of these shrublands being burnt in wildfires between ~1969 and 2004 (Braun 2006). The most recent fires occurred between 2000 and 2004 inclusive, and the oldest mapped fire scar is dated 1969, which is a collection of fire scars visible on the earliest aerial photography available for the study site (1969) and represents a number of fires of similar age from around that time (Braun 2006). Fires in the study region predominantly occur in the sandplain shrublands, with the woodlands remaining largely unburnt, except at the edges, because the woodlands lack the dense flammable understorey found in the shrublands (Braun 2006).

The shrublands generally contain a single dense band of vegetation that increases in height with time since fire and contains limited vegetation cover beneath it (Parsons & Gosper 2011; Dalglish et al. 2015). Recently burnt areas (8–14 years since last fire) are short (< 2 m) and lack a litter layer and distinct canopy (Figure 1.2). The long unburnt shrublands (34–49 years) are characterised by variable structure between 0 and 4 m, although the most dense vegetation is between 0 and 2 m, whereas the very long unburnt shrublands (> 50 years) are more open in the 0 to 2 m stratum and more dense between 2 and 4 m, and also exhibit greater patch size variability (Figure 1.2) (Dalglish et al. 2015).

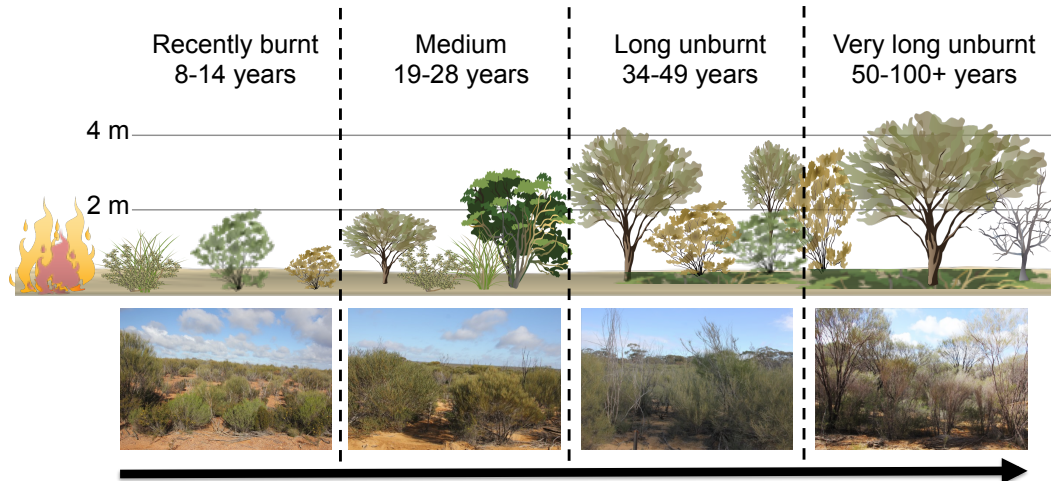


Figure 1.2 Changes in shrubland structure with increasing time since fire. Clipart images are sourced from the Integration and Application Network (www.ian.umces.edu/symbols/). NB: Due to spatial and temporal variation in sampling strategies, some parts of the thesis refer to ‘recently burnt’ vegetation that was 10–13/14 years old.

Fauna

The reserve contains 74 reptile, 27 mammal, 143 bird and six frog species (BHA, *unpublished data*). Several species are at the edge of their range here because the location is transitional between the arid interior and more mesic southwest of the state (Richards et al. 2011a; Richards et al. 2011b). Most medium and large native mammal species (> 500 g body weight) have become extinct in the region (Woinarski et al. 2014), with the only extant species being the long-beaked echidna *Tachyglossus aculeatus*, the euro *Macropus robustus*, the western grey kangaroo *Macropus fuliginosus*, the red kangaroo *Macropus rufus*, and the dingo *Canis dingo*. Introduced mammals that occur at the reserve include the feral cat, red fox, European rabbit, house mouse *Mus musculus* and goat *Capra hircus*. The nationally threatened malleefowl *Leipoa ocellata* occurs at the reserve and is threatened by inappropriate fire regimes and introduced predators (Benshemesh 2007).

Chapter 2.

A critical review of habitat use by feral cats and key directions for future research and management

Doherty TS, AJ Bengsen and RA Davis (2014) *A critical review of habitat use by feral cats and key directions for future research and management*. *Wildlife Research*, 41:435–446.

Introduction

Invasive mammalian predators have caused or contributed to the decline and extinction of many species worldwide (Salo et al. 2007). Examples include the red fox *Vulpes vulpes* (Johnson 2006), mustelids (Mustelidae) (King & Moody 1982; Salo et al. 2010), rats *Rattus* spp. (Jones et al. 2008; Capizzi et al. 2014) and the domestic cat *Felis catus* (Medina et al. 2011; Duffy & Capece 2012). Humans have introduced the domestic cat to almost every region of the world and self-sustaining wild populations now exist in a wide variety of landscape types including deserts, forests and tropical to sub- Antarctic islands (Long 2003). Animals in these populations are generally termed ‘feral’, meaning that they are descended from domesticated ancestors but now exist in a free-living state with no direct dependence on humans. Feral cats are distinguished from ‘unowned’ cats (stray or semiferal) in that unowned cats remain dependent on humans for at least the incidental provision of resources such as food or shelter.

Feral cats are almost exclusively carnivorous and generally obtain most of their food resources by hunting live prey (Fitzgerald & Turner 2000). Feral cats are acknowledged as one of the world’s worst 100 invasive species (Lowe et al. 2000) and are thought to have been an important contributing factor to at least 14% of bird, reptile and mammal extinctions globally (Medina et al. 2011) and at

least 16 mammal extinctions in Australia² (Johnson 2006). Predation by feral cats can jeopardise conservation programmes aiming to reintroduce native fauna into areas of their former range (Moseby et al. 2011b; Potts et al. 2012), and cats can have non-lethal impacts on susceptible populations through competition, disease transmission, induced predator-avoidance behaviour and hybridisation (Daniels et al. 2001; Medina et al. 2014). Reducing the impacts of feral cats is a priority for conservation managers in Europe (Daniels et al. 2001; Sarmiento et al. 2009), North America (Blancher 2013; Loss et al. 2013), Oceania (Medway 2004; Woinarski et al. 2011; Garnett et al. 2013) and islands worldwide (Keitt et al. 2002; Judge et al. 2012; Nogales et al. 2013).

Substantial effort has been invested in research and management to mitigate the impacts of feral cats in recent years (e.g. Moseby et al. 2009b; Hess et al. 2009; Luna-Mendoza et al. 2011). Cats have been eradicated from 105 mostly small islands (DIISE 2014), but unfenced mainland sites generally require sustained control efforts because cats have a high reproductive output and an aptitude for reinvasion (Bowen & Read 1998; Short & Turner 2005). The development of efficient and effective management programmes for invasive predators such as feral cats usually requires reliable information about the spatial ecology of the subject species to inform management decisions such as the density at which control devices should be deployed (Goltz et al. 2008; Moseby et al. 2009b) or the geographic scale of control operations (Mosnier et al. 2008). Information about habitat use is particularly important for maximising the rate at which pest species encounter control devices such as traps or poison baits (Recio et al. 2010; Bengsen et al. 2012), designing efficient monitoring programmes (Pickerell et al. 2014), predicting the spatial distribution of an invasive species' impacts (Kliskey & Byrom 2004) or identifying native fauna populations that are most likely to be imperilled by the invader (Gehring & Swihart 2003; Recio et al. 2014).

Given the growing recognition of the impact of feral and unowned cats and developments in the technology available to both monitor and control them (e.g.

² This number has since been revised to 22 by Woinarski *et al.* (2015) to reflect taxonomic changes and other new information.

Algar et al. 2007; Recio et al. 2010; Bengsen et al. 2011), it is timely to review the state of knowledge on the habitat use patterns of cats across their broad global distribution. Here, we review experimental and observational studies conducted around the world over the last 35 years that aimed, at least in part, to examine habitat use by feral and unowned cats. The term 'habitat use', as used here, refers to the habitat components and vegetation types that an animal uses, whereas 'habitat selection' refers to the behavioural process that ultimately produce habitat use patterns, and is usually described as preference or avoidance of different habitat components or vegetation types (Johnson 1980; Hall et al. 1997). Our aim here is not to provide strict guidelines for research and management of feral cats because this is not feasible or useful, given their global distribution and the wide range of contexts in which they occur. Rather, we seek to establish a conceptual framework that will guide the activities of researchers and land managers in reducing feral cat impacts at a scale appropriate for useful management and research. Specifically, our aims are to: (1) summarise the current body of literature on habitat use by feral and unowned cats in the context of applicable ecological theory (i.e. habitat selection, foraging theory); (2) develop testable hypotheses to help fill important knowledge gaps in the current body of knowledge on this topic; and (3) build a conceptual framework that will guide the activities of researchers and managers in reducing feral cat impacts. Most of the available literature is on feral cats, rather than unowned cats, so we generally refer to them collectively as feral cats throughout.

Methods

We searched Web of Science and Scopus international databases for studies on habitat use by feral and unowned cats with combinations of the following keywords: feral cat, *Felis catus*, stray cat, semi-feral, free-living, habitat use, habitat selection, and home range. To these results, we added any additional studies on cat habitat use that we sourced from reference lists, book chapters and publically available theses. After removing duplicates, we also excluded studies that did not include a component on habitat use by *Felis catus*, and studies that did not include feral or unowned cats, resulting in a list of 27 studies published between 1979 and 2014 (Figure 2.1).

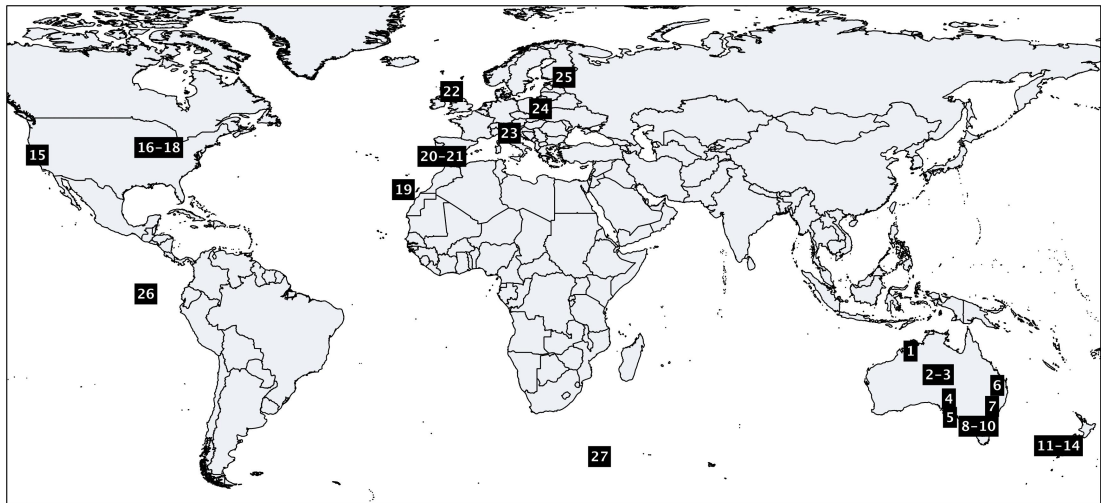


Figure 2.1 World map showing the locations of the reviewed studies on habitat use by feral and unowned cats (*Felis catus*). Numbers refer to studies listed in Table 2.1.

The small number of studies available ($n = 27$) meant that a quantitative analysis of observed patterns was not possible. Instead, we examined habitat use within home-ranges and collated information for each study to describe survey methods, observed patterns of irregular habitat use (resulting from apparent habitat preferences or aversions), and any factors that were believed to be responsible for the observed patterns of habitat use. We classified these factors as one or more of the following: none; prey availability; intraguild predation/competition; shelter availability; or human resource subsidies. We also graded the ability of each study to identify those factors responsible for observed patterns using five levels: (1) supposition – no data or references to support contentions; (2) supposition based on casual observation of apparent coincidence, e.g. predators or prey more abundant in one habitat component, but supporting data are not provided; (3) supposition based on casual observation of apparent coincidence and supporting data provided; (4) manipulative study without experimental controls or replicates; (5) manipulative study with experimental controls and replicates.

To describe broad patterns in cat habitat use we recorded the frequency of studies where cats favoured or avoided the following seven broad habitat components within their home ranges: forest (~30–100% tree cover); woodland (~10–30%); shrub/heathland; grassland; riparian areas; infrastructure (farm buildings, urban and industrial areas); and agricultural land (fields, pasture, paddocks and crops). We did not include habitat components that fell outside of

these groups and were reported in only one or two studies (e.g. mudflats, swales, refuse dumps, dunes) or habitat components that were too broad or ambiguous for classification (e.g. open areas, small and large remnant patches, adjacent slopes, steep slopes). We did not focus on intrahabitat use (e.g. microhabitats) because few studies recorded information at this resolution and we note that it is difficult to collect such fine-scale information for wide-ranging carnivores like feral cats. Some studies qualified for both avoidance and preference of one habitat component (e.g. favoured deciduous forest and avoided pine forest). These frequencies are for comparative purposes only, as we recognise that preference or avoidance of different habitats depends largely on the availability of other habitat components in a study landscape. All favoured or avoided habitat components are listed in Table 1 as they appear in the studies.

Results

Of the 27 studies reviewed, 74% were solely on feral cats and 11% were a mixture of feral, unowned and owned (pet) cats. We also included two studies where the group of study animals were a mixture of feral *Felis catus* and the closely related native *F. silvestris*, and two studies that were on unowned cats only. We treated Recio and Seddon (2013) and Recio *et al.* (2014) as a single study because they used the same dataset.

VHF or GPS tracking was used to study cat space use in 70% of studies, with sample sizes ranging from four to 32 animals (mean $13.8 \pm 1.8 SE$). Of the eight studies that did not track individual cats, three used tracking stations with visual or scent- based lures (active tracking stations), whereas the remaining studies used scat counts, visual surveys or passive tracking stations (Table 2.1). We assume that habitat use patterns identified in these studies represent the results of habitat selection within home ranges.

Patterns of habitat use

In all, 37% of studies were from Australia, 15% from New Zealand, 22% from the UK and Europe, 15% from the USA and one study each from the Galapagos Islands, Canary Islands and Marion Island (Figure 2.1). Of the studies, 22% were conducted on islands and the rest were continental. Nine studies had temperate marine/maritime climates, five were Mediterranean, four were

warm/hot summer continental, three each were humid subtropical or arid, two had a steppe climate and one had a tundra (sub-Antarctic) climate (Table 2.1). Around half of the studies (13) were conducted in a mixed landscape of native vegetation and agricultural land and/or urban areas, and the remainder (14) were conducted solely in vegetated/natural areas (Table 2.1).

The habitat components most commonly reported as being favoured by cats were infrastructure (26% of studies), riparian areas (22%), and agricultural land and shrub/heathlands (18.5% each; Figure 2.2). The most commonly avoided habitats were agricultural land (26%) and grassland (11%; Figure 2.2). Cats used a diverse range of habitats including but not limited to arid deserts, shrublands and grasslands, fragmented agricultural landscapes, glacial valleys, equatorial to sub-Antarctic islands, urban areas and a range of different forest and woodland types (Table 2.1). Use of linear features such as tree lines and road verges was recorded in four studies, all of which were conducted in mixed agricultural landscapes, and five studies suggested that feral cats exploit different habitat components to meet different activity requirements, such as hunting or resting.

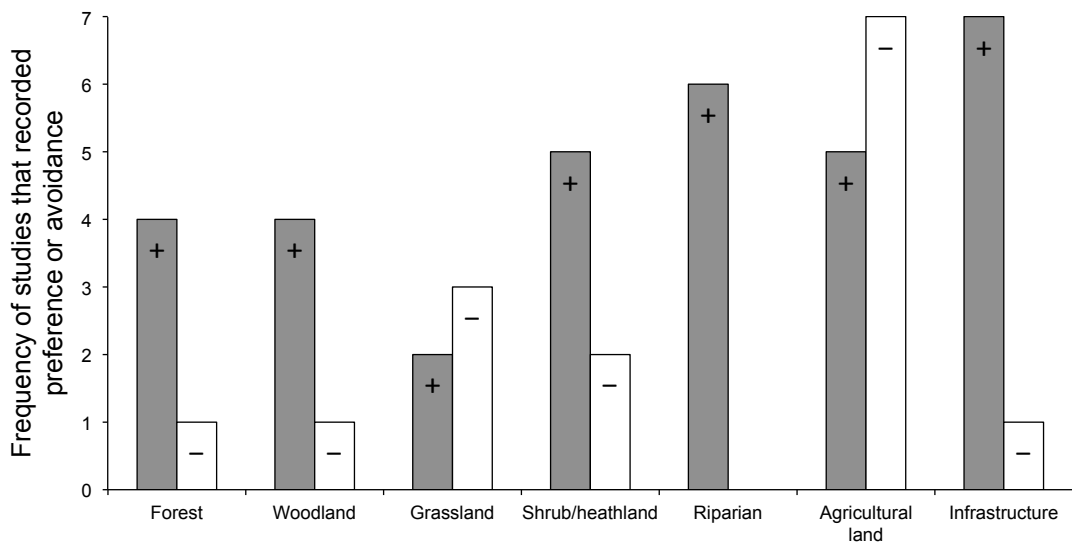


Figure 2.2 Frequency of studies where cats favoured (grey bars with + symbol) or avoided (white bars with - symbol) seven broad habitat components: forest, woodland, grassland, shrub/heathland, riparian areas, agricultural land, and infrastructure.

Strength of inference

Overall, most studies provided weak or no data to support their perceptions about the factors driving habitat use by cats (78% Level 1 or 2) (Figure 2.3). 19% of studies provided some data to support their inferences (Level 3), but only one study conducted a manipulative experiment (Level 5). 59% of studies posited that prey availability influenced cat habitat use, but only 20% of those studies provided data to support this idea (Figure 2.3). 11% of studies suggested that human resource subsidies influenced cat habitat use and 37% suggested that shelter availability influenced habitat use, but only one provided supporting data (Figure 2.3). Predation/competition was put forward as a determining factor by 26% of studies, around half of which provided data to support those inferences: three with data on variation in predator abundance or activity among habitat components and one study that undertook a landscape-scale manipulative experiment with controls and replicates. Five studies made no inferences as to the mechanisms influencing cat habitat use (Figure 2.3).

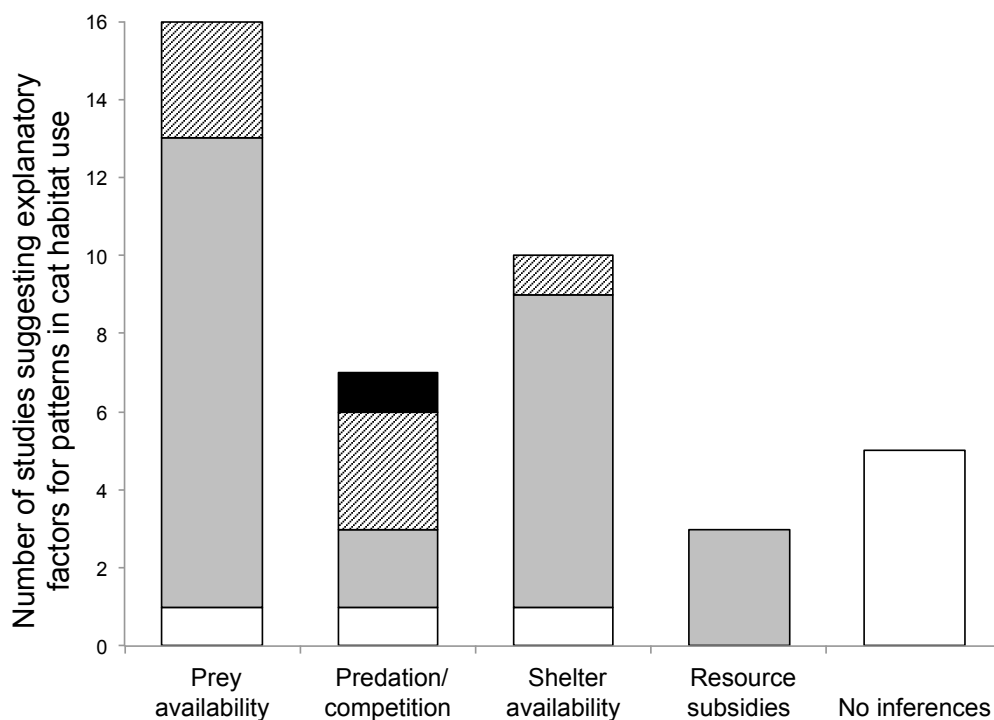


Figure 2.3 Frequency of studies suggesting factors that may explain observed patterns in cat habitat use: Level 1 (solid white); Level 2 (solid grey); Level 3 (diagonal stripe); Level 5 (solid black). No studies were classed as Level 4.

Table 2.1 Summary information for the 27 studies reviewed here on habitat use by feral and unowned cats *Felis catus*.

Study # ^A	First author	Year	Location	Climate ^B	Landscape type	Survey type	Analysis ^C	Favoured habitat	Avoided habitat	Hypothesised structuring factors	Strength of inference for structuring factors ^D
1	McGregor	2014	Central Kimberley, Australia	Steppe	Tropical grasslands	GPS tracking	Discrete choice modelling and multimodel inference	Open areas, edges, recently burnt and/or grazed areas, riparian areas and water.	Higher elevations	Prey	3
2	Edwards	2002	Northern Territory, Australia	Desert (arid)	Arid	Passive tracking station	Chi-square GOF	Mulga woodland	Grasslands	Prey	2
3	Mahon	1998	Simpson Desert, Australia	Desert (arid)	Arid	Passive tracking station	Chi-square GOF	Dune crests	-	Prey None	1 n.a.
4	Moseby	2009	Roxby Downs, Australia	Desert (arid)	Arid	GPS tracking	Compositional analysis	Dunes, creekline	Swales	Prey Shelter None	2 2 n.a.
5	Bengsen	2012	Kangaroo Island, Australia	Mediterranean	Mixed agricultural, island	GPS tracking	Chi-square GOF	Mixed shrub and woodland, woodlands	Low and medium woodlands, open paddocks	None	2
6	Graham	2012	Queensland, Australia	Humid subtropical	Mixed agricultural	Active tracking station	Occupancy	Agricultural land, large remnant edges, roadside verge remnants	Interior of small and large remnant patches	Shelter	2
7	Molsher	1999	Lake Burrendong, Australia	Humid subtropical	Temperate woodlands	VHF tracking	Compositional analysis	Open woodland (landscape scale), grasslands (home-range scale)	Mudflats (both scales)	Prey Shelter	2 2
8	Buckmaster	2012	Gippsland, Australia	Marine temperate	Tall forest	VHF and GPS tracking	Logistic regression	Creeklines	n.a.	Prey Predation/competition	5
9	McTier	2000	French Island, Australia	Marine temperate	Mixed agricultural, island	VHF tracking	Chi-square	Bushland, roadsides, buildings	Grasslands	Predation/competition Shelter	2 2
10	Hutchings	2000	Angelsea Tip, Australia	Marine temperate	Refuge site, mixed	VHF tracking, spotlighting	Chi-square	Heathland (day), refuse dump (night)	Heathland (night), refuse dump (day)	Shelter Prey	2 2
11	Recio	2010	Tasman Valley, New Zealand	Maritime temperate	Glacial valley and riverbed	GPS tracking	Compositional analysis and Chi-square GOF	Mature riverbed	Adjacent slopes	Shelter	1
12	Recio	2013 and 2014	Godley Valley, New Zealand	Maritime temperate	Glacial valley and riverbed	GPS tracking	Logistic regression	Shrub and pasture cover, lower elevations, bare ground on slopes	n.a.	Prey	2
13	Harper	2007	Stewart Island, New Zealand	Maritime temperate	Island	VHF tracking	Compositional analysis	Tall podocarp–broadleaf forest	Sub-alpine shrubland, alpine heath	Shelter Prey	3 3
14	Alterio	1998	Boulder Beach, New Zealand	Maritime temperate	Coastal, mixed agricultural	VHF tracking	Chi-square GOF	Ungrazed areas, dunes	Grazed areas, grasslands	Prey	2
15	Hall	2000	California, USA	Mediterranean	Mixed agricultural	VHF tracking	Chi-square GOF	Riparian, buildings	Annual crops, perennial crops	Shelter Prey	1 1

Study # ^a	First author	Year	Location	Climate ^b	Landscape type	Survey type	Analysis ^c	Favoured habitat	Avoided habitat	Hypothesised structuring factors	Strength of inference for structuring factors ^d
16	Gehring	2003	Indiana, USA	Hot summer continental	Mixed urban-agricultural	Active tracking station	Logistic regression	Higher canopy cover, lower ground cover, lower diversity of habitat, smaller patch area, greater human development, presence of corridors	Fields	None	n.a.
17	Horn	2011	Illinois, USA	Hot summer continental	Mixed urban-agricultural	VHF tracking	Compositional analysis	Grasslands, forests, industrial areas, row crops (summer only)	Row crops (autumn, winter)	Shelter	2
18	Gehrt	2013	Chicago, USA	Hot summer continental	Mixed urban-natural	VHF	Euclidean distance-based selection ratios	Urban land	-	Prey	2
19	Medina	2007	Canary Islands, Spain	Mediterranean	Island	Scat survey	Kruskal-Wallis	None	None	Predation/competition	3
20	Ferreira	2011	Portugal	Mediterranean	Mixed agricultural	VHF tracking	Compositional analysis	Farms, areas within 200 m of roads, smaller slopes	Steep slopes, areas >200 m from roads, native vegetation	Prey	2
21	Lozano	2003	Iberian Peninsula	Mediterranean	Mountainous	Scat survey	PCA and regression	High rabbit abundance, scrub-pastureland mosaic, high scrub cover and shelter availability	n.a.	Human resource subsidies	2
22	Daniels	2001	Scotland, UK	Maritime temperate	Highlands	VHF tracking	Compositional analysis	Woodland, stream edge	Pasture, heather	Prey	2
23	Genovesi	1995	Italy	Humid subtropical	Mixed agricultural	VHF tracking	Chi-square GOF	Arboreal shelter belts, reed thickets, riparian vegetation	Open cultivated fields	None	n.a.
24	Krauze-Gryz	2012	Poland	Marine temperate	Mixed agricultural	Active tracking station	Occupancy	Forest	Open areas	Predation/competition	3
25	Holmala	2009	Finland	Warm summer continental	Mixed agricultural	VHF tracking	Wilcoxon signed-rank test	Fields, open areas, young and mature deciduous forest	Mature pine and mixed forests	Human resource subsidies	2
26	Konecny	1987	Galapagos Islands, Ecuador	Steppe (arid)	Island	VHF tracking	Contingency table	Lava/shrub	-	Prey	2
27	van Aarde	1979	Marion Island, South Africa	Tundra (sub-Antarctic)	Sub-Antarctic island	Observation	t-tests	Coastal habitat types	Barren lava fields	Prey	2

^a Identification numbers for studies that contained a mix of feral, owned and unowned cats: 15, 23 and 24; a mixture of *F. catus* and *F. silvestris*: 20 and 21; and unowned cats only: 16 and 19. All other studies were

conducted on feral cats only.

^b Climates were categorised according to the Köppen-Geiger classification system (Wilkerson & Wilkerson 2010).

^c GOF, goodness of fit; PCA, principal component analysis.

^d Strength of inference rating: (1) supposition - no data or references to support contentions; (2) supposition based on casual observation of apparent coincidence e.g. predators or prey more abundant in one habitat component, but supporting data is not provided; (3) supposition based on casual observation of apparent coincidence and supporting data provided; (4) manipulative study without experimental controls or replicates; (5) manipulative study with experimental controls and replicates.

Discussion

Feral and unowned cats occur in a wide range of biomes and climatic zones, within which individual cats may have access to a limited range of macro-habitat components or vegetation types. It is therefore not possible or useful to make broad generalisations about preferential use or avoidance of specific habitat components. However, the combined results of all studies suggest that feral cats generally favour structurally complex habitat components over simpler ones. For example, most studies showed that cats or their sign were more likely to be recorded in vegetation types characterised by a mixture of plant growth forms close to ground level, such as mixed shrublands and woodlands, than vegetation types characterised by an open or homogenous structure, such as mature pine forests or grasslands (e.g. Horn et al. 2011; Bengsen et al. 2012). Several studies also found that cats were more likely to be recorded at the edges of vegetation patches, or along linear features such as road verges or creeks that traversed patches, than in the patch interior (e.g. Gehring & Swihart 2003; Graham et al. 2012; Pastro 2013). Only three studies showed contradictory patterns, in which cats were more likely to be recorded in open country than in structurally complex vegetation. One study in northern Australia found that cats favoured areas characterised by open grass cover and suggested that this was probably due to increased hunting success (McGregor et al. 2014). However, that study only considered habitat use by moving cats and discarded data that was deemed to represent cats at rest. A further two studies from Europe found that cats were more likely to be recorded in open country around farm houses that supplied them with food, than in native vegetation (Holmala & Kauhala 2009; Ferreira et al. 2011), although one of these did show a preference for patch edges over interior (Ferreira et al. 2011).

Most studies made inferences based on four mechanisms hypothesised to influence habitat use by feral cats: prey availability; shelter availability; predation/competition; and human resource subsidies. The hypothesised role of prey availability in structuring habitat use is supported by models of predator-prey habitat selection and optimal foraging theory (Pyke 1984; Mitchell & Powell 2004; Börger et al. 2008). Flaxman and Lou (2009) posited that predators preferentially use landscape elements associated with either high prey densities

(‘prey tracking’), or with high densities of the prey’s resources (‘resource tracking’ – an indirect way of identifying where prey will occur). None of the studies experimentally tested these ideas, although one study (Recio & Seddon 2013; Recio et al. 2014) found that feral cat home ranges tended to be concentrated on habitat types characterised by high suitability for rabbits – their key prey species in the area. Intraguild predation and competition can also play a key role in structuring habitat use across a range of marine and terrestrial taxa (Polis & Holt 1992; Ritchie & Johnson 2009), and this may hold for feral cats where they occur with higher-order predators. For example, Molsher (1999) found that cats increased their use of open grasslands (which were thought to be more profitable foraging areas) after the density of foxes using those areas was reduced. Similarly, in an arid environment, Brawata and Neeman (2011) found that feral cats were more likely to be detected close to artificial watering points at sites where dingoes were subjected to lethal control, than at sites where they were not. Other studies have also found that cats were observed less frequently at sites where larger carnivores were more common (Brook et al. 2012; Krauze-Gryz et al. 2012; Lazenby & Dickman 2013). Temporal segregation between cats and larger carnivores also suggests that intraguild predators can influence the activity times of feral cats (Brook et al. 2012; Wang & Fisher 2013). The effect of intraguild predation on habitat use is closely linked with that of shelter availability. Meta-analysis has shown that prey experience less intraguild predation in more structurally complex habitats (Janssen et al. 2007), so shelter availability is likely to play a key role in providing feral cats with protection from larger predators, including humans. However, the cases recorded here of humans influencing cat habitat use were all in a positive direction, since all of those studies contained at least some unowned cats that were potentially fed by humans (Holmala & Kauhala 2009; Ferreira et al. 2011; Krauze-Gryz et al. 2012). Nonetheless, humans could also be considered an apex predator with potentially prohibitive effects on cat habitat use. Hutchings (2000) discussed the possibility of such an interaction for cats at a municipal refuse site, but no study investigated this in detail. Availability of shelter may also provide cats with protection from environmental stressors such as inclement weather (Harper 2007). In reviewing their own results and previous studies, Lozano *et al.* (2003) concluded that cats need two specific habitat types: closed habitats for shelter and resting, and open areas for hunting. In that

study, the occurrence of 'wild-living' cats (feral *F. catus* and native *F. silvestris*) was positively related to scrub–pastureland mosaics and areas with high rabbit abundance, and microhabitats with high shrub cover and availability of shelter. Similar inferences were made in four other studies (Genovesi et al. 1995; Molsher 1999; Hall et al. 2000; Hutchings 2000), and we term this 'behaviourally-stratified' habitat use.

These general patterns of cat habitat use can be related to the known hunting behaviour of cats. Domestic cats are solitary hunters that rely mainly on sight and sound to detect their prey (Bradshaw 1992). Fitzgerald and Turner (2000) described two primary hunting techniques: 'mobile', whereby the cat moves around an area of habitat seeking out prey, and 'stationary', where the cat waits at a point of interest, such as the entrance to a rabbit burrow, and ambushes its prey upon appearance. These two techniques aren't mutually exclusive and both rely heavily on stealth. The general pattern of feral cats using habitats with a mixture of vegetation cover at ground level is likely to improve hunting success by providing cats with a mixture of both cover and open areas in which they can observe, stalk and then ambush their prey. The 'habitat heterogeneity hypothesis' also predicts that, in many cases, these areas may support a greater diversity and density of potential prey than more homogeneous habitat components (Tews et al. 2004). Edge habitats, linear features, and riparian vegetation are similarly likely to improve hunting success. For example, Pastro (2013) found that feral cats were recorded more frequently at the ecotone between burnt and unburnt grasslands than in continuous areas of habitat. In this regard, dense homogeneous habitats where a cat's visual detection ability would be compromised are likely to be unfavourable areas for hunting by feral cats. In contrast, McGregor *et al.* (2014) found that feral cats in tropical savannas actively chose areas with high prey abundance that had been recently burnt or grazed and posited that the reduced vegetation cover improved cats' hunting success. In future, an improved understanding of how habitat use by feral cats is influenced by their hunting behaviour could be achieved by undertaking within-habitat analyses of vegetation composition. This might include consideration of patch structure, edge availability and cover continuity.

The strength of evidence available for factors explaining habitat use was generally low in the studies we examined, with 78% of cases providing little or no data to support their inferences. Most studies examined habitat use using radio-tracking and employed observational or correlative data on other variables to explain these patterns. These types of studies have poor inferential capabilities because they generally involve multiple confounding and interactive explanations for the observed patterns and are hence unable to demonstrate cause and effect. Additionally, few studies acknowledge the limitations of their conclusions. The strongest inferences are gained through 'classical experiments', i.e. those that employ treatment and nil-treatment areas and are replicated and randomised, or other types of experiments that lack either replication or randomisation (Hone 2007). Only one study used this kind of approach (Molsher 1999).

Conceptual model

The low inferential capacity of the studies reviewed here also limits our ability to make generalisations about the mechanisms influencing habitat use by feral cats. However, by drawing on ecological theory and published literature on other medium-sized carnivores, we have been able to propose a conceptual framework for this topic. Such theoretical frameworks have been developed to explain predator-prey habitat use and dynamics (Polis & Holt 1992; Holt & Polis 1997; Heithaus 2001; Rosenheim 2004). For example, game-theoretic models predict that mesopredators should preferentially use habitat that reduces the risk of predation from apex predators, rather than habitat with high prey availability, when dietary overlap between the two predator levels is high and when the apex predators are efficient competitors (Heithaus 2001). Several studies of mammalian predators have reported results consistent with these predictions (Thompson & Gese 2007; Wilson et al. 2010), and the same might be expected for feral cats in many situations (e.g. Molsher 1999). However, cats also commonly occur as apex predators, particularly on islands (e.g. Rayner et al. 2007), in which case patterns of space use and habitat selection should largely be determined by resource availability (Heithaus 2001). Excluding humans, cats were the top predator in the six island studies reviewed here, and five of those studies asserted that prey and/or shelter availability determined cat habitat use. For example, on Stewart Island in New Zealand, Harper (2007) found that cats preferred to use podocarp-

broadleaf forests where shelter from inclement weather was most available, and used the less protective and less preferred subalpine shrubland significantly more on dry days than on wet days.

We developed a conceptual model to explain patterns in cat habitat use (Figure 2.4). The relationships that we discuss here warrant further examination, given the speculative nature of this model and the knowledge gaps that we have previously identified. We propose that ecosystem components that influence habitat use (A in Figure 2.4: predators, prey, shelter and resource subsidies) are hierarchically structured, with predation/competition exerting the strongest influence, and other factors increasing in importance where predators are absent (Thompson & Gese 2007; Ross et al. 2012). We also expect that habitat choices are behaviourally stratified (B in Figure 2.4), with dense habitats used for shelter and more open habitats used for hunting prey (Lozano et al. 2003). Broad vegetation types or habitat components that are generally favoured (but not exclusively) include infrastructure, riparian areas, shrub/heathland, forests and woodland, while agricultural land is generally avoided, as are grasslands to a lesser extent (but not exclusively) (C in Figure 2.4).

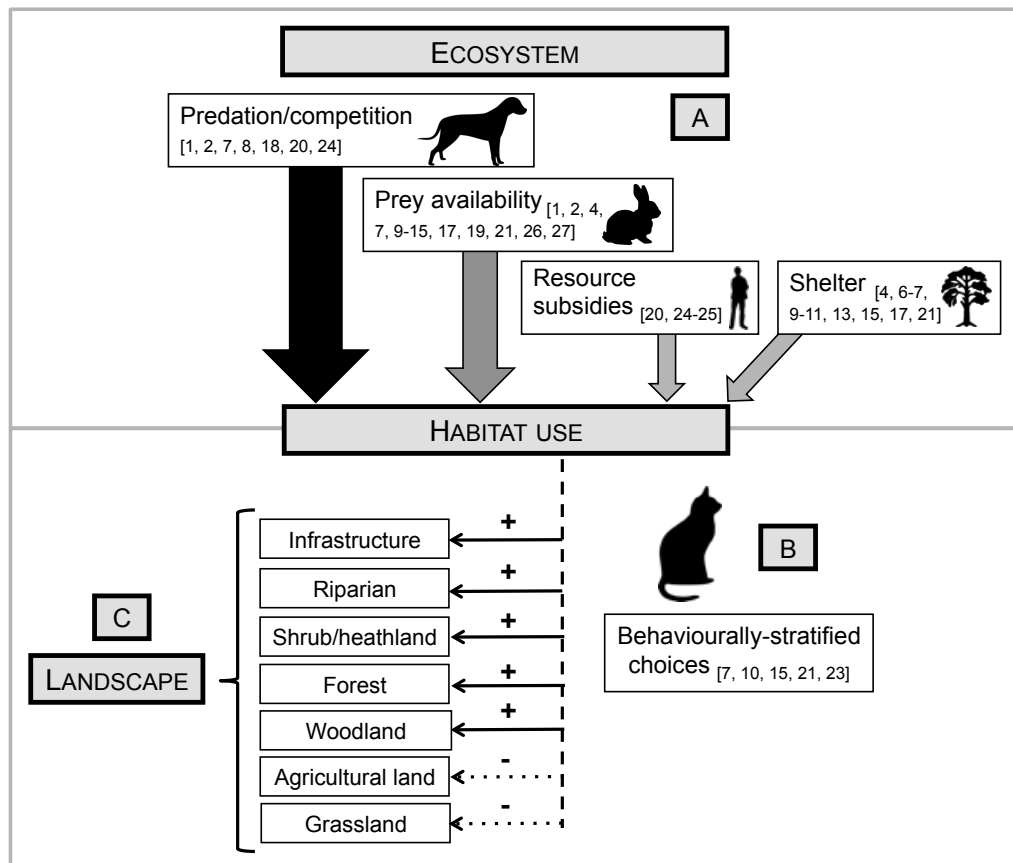


Figure 2.4 Conceptual model to describe factors that can potentially influence habitat use by feral cats. Ecosystem components that influence habitat use are hierarchical (A), i.e. predators have a stronger influence than prey, but prey increases in importance where predators are absent. Habitat choices are behaviourally stratified (B) and broad habitat components that cats favour (+) or avoid (-) are nested in the landscape (C). Studies that provide support for or inferences regarding each component are listed using subscripts that correspond to study numbers in Table 2.1.

To aid in validating this model, we developed testable hypotheses for further investigation: (1) higher-order predators with a high dietary overlap with feral cats and strong competitive ability will have spatially or temporally prohibitive effects on cat habitat use (Heithaus 2001; Wilson et al. 2010; Ross et al. 2012); (2) where higher-order predators exclude feral cats from using areas with optimal prey availability, removal of those predators will allow cats to expand their use of optimal prey habitat (Molsher 1999; Ritchie & Johnson 2009; Prugh et al. 2009); (3) prey and/or shelter availability will be the most important factors influencing cat habitat use where higher-order predators are absent (Heithaus 2001).

Key directions for future feral cat research and management

Because feral cats occur in a wide range of ecological contexts and show high variability in many population-specific traits, including those related to spatial ecology and habitat use, cat-management programmes should be designed to account for site-specific conditions (Dickman et al. 2010a; Appendix A). Future research and management to ameliorate the damage caused by feral cats will benefit from an integrated conceptual framework that facilitates the identification, development and evaluation of site-specific management activities. Consequently, in Table 2.2 we provide a list of key directions that will assist conservation managers and researchers in better understanding and ameliorating the impact of feral cats at a scale appropriate for useful management and research, and we discuss these in detail below.

Table 2.2 Key directions for future research and management that aims to understand and ameliorate the impact of feral cats.

Management

- Incorporating information on spatial and temporal variation in prey availability should benefit control programmes by enhancing the efficiency and effectiveness of control and monitoring activities.
- Control programmes should consider the presence of higher order predators and the effects they may have on habitat use by cats.
- Active monitoring of management actions is essential for the continual improvement of control programmes and to ensure that effort is not wasted. Continual improvement may be best achieved by using an adaptive management framework that evaluates assumptions about habitat use by cats and the ability of control activities to impact on the population.

Research

- Should use experimental approaches and ecological theory to develop and test hypotheses regarding predator-prey dynamics and intra-guild interactions.
 - The strongest evidence will be gained from replicated landscape-scale experiments where the densities of predators, prey or competitors are manipulated and then the response in cat habitat use is measured.
 - As far as possible, studies should:
 - Relate habitat use patterns of cats to variability in the abundance or activity of cat prey species and sympatric predators.
 - Be conducted over temporal scales appropriate to the study's aims.
 - Aim to examine habitat use by feral cats in landscapes that are poorly represented in the existing literature.
-

Apex predators may play an important role in structuring habitat use by feral cats in some cases, but additional research is needed to establish how the strength of this mechanism varies across a range of different systems. Interference competition can have spatially or temporally prohibitive effects on habitat use by cats (Molsher 1999; Krauze-Gryz et al. 2012) and, although untested, larger predators might therefore help exclude feral cats from areas inhabited by threatened prey species. Apex predators are declining across the globe (Ripple et al. 2014) and loss of top predators can lead to mesopredator release of cats and more intense impacts on native fauna (Crooks & Soulé 1999; Risbey et al. 2000), although it is often difficult to clearly attribute causation in mesopredator release studies (Prugh et al. 2009; Allen et al. 2012). Conservation managers should consider apex predators as a possible tool for ameliorating feral cat impacts (Ritchie et al. 2012; Letnic et al. 2012), but must also consider potentially conflicting social, economic and other biodiversity conservation concerns (Fleming et al. 2012).

Linear features are used by feral cats in fragmented production landscapes, and cats can benefit from fragmentation when native carnivores do not (Crooks 2002). The use of tree lines, road verges and other corridors suggests that control devices could be deployed in these areas to maximise their encounter rate by cats, and hence maximise the efficacy and efficiency of control or monitoring programmes (Bengsen et al. 2012). Although, in arid areas where vegetation contrasts are less extreme, roads may be less important (Mahon et al. 1998; Read & Eldridge 2010). Since our review shows often-divergent outcomes in the use of similar habitat components or vegetation types worldwide, active monitoring and evaluation of expectations is essential for developing effective and efficient control programmes. Also, given that prey availability appears to be an important determinant of cat habitat use, incorporating information on spatial and temporal variation in prey availability should benefit control programmes (Christensen et al. 2013; Recio & Seddon 2013; Recio et al. 2014), particularly in situations where cats are the dominant predator.

Our review has revealed that the standard of evidence available to explain patterns of cat habitat use is generally low. There is a risk that an accumulation of weak evidence will be mistaken for the existence of strong evidence. Given that a

sound understanding of the habitat-use patterns of feral cats is often an important precursor to effective mitigation of their impacts, and that most of our current understanding is based on observational studies involving multiple confounding and interactive explanations for observed patterns, there is a clear need for more rigorous approaches to future studies. To adequately address the range of possible explanations, future studies should, where possible, use rigorous, experimental approaches and ecological theory to develop and test hypotheses regarding predator–prey dynamics and intraguild interactions. Also, studies should ideally incorporate information on spatial and temporal variation in the activity or abundance of cat prey species and sympatric predators (Dickman 1996a) and be conducted over appropriate temporal scales to account for potential biases caused by changes in predator behaviour or prey and shelter availability (Cruz et al. 2013). The spatial and temporal scales needed for such experiments make them expensive and logistically difficult (Glen et al. 2007), although not impossible (e.g. Molsher 1999). Studies should also aim to examine habitat use by feral cats in landscapes such as rainforests, salt marshes and alpine habitats, which are poorly represented in the existing literature. An improved understanding of habitat use by feral cats is key to reducing their impact on native species across the globe.

Acknowledgements

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Chapter 3.

Overlap in the diet and habitat use of feral cats and dingoes at a semi-arid rangeland site

Doherty TS (2015) *Dietary overlap between sympatric dingoes and feral cats at a semi-arid rangeland site in Western Australia*. *Australian Mammalogy*, 37:219–224.

Introduction

Invasive predator control programmes aiming to limit predation of prey species generally use shooting, trapping or poison baiting to reduce predator population densities. Effective control programmes for feral cats require a detailed understanding of their movements and habitat use (Bengsen et al. 2012; Oppel et al. 2014). For example, Bengsen et al. (2012) used movement data to recommend that control devices should be deployed at a density no less than 1.7 devices km⁻² at Kangaroo Island in Australia. Recio et al. (2014) found that cats in New Zealand situated their home ranges over areas of high habitat suitability for rabbits *Oryctolagus cuniculus*—their primary prey in the region—so the authors suggested that cat population control could be improved by focussing control efforts on areas of high rabbit density. Also in New Zealand, cats preferentially used ungrazed compared to grazed areas (Alterio et al. 1998), hence also suggesting the need to concentrate management efforts where cats are most active.

Given the behavioural plasticity of cats and the wide range of environments in which they exist (Chapter 2), it is not feasible or useful to make broad generalisations about preferential use or avoidance of certain habitat types. Although, in Chapter 2 I showed that cats were generally recorded most often in habitat types characterised by a mixture of plant growth forms close to ground level. Also, I identified the principal factors likely to influence cat habitat use as predation and competition, prey availability, shelter availability, and provision of

resources by humans. Importantly though, the relative importance of each factor is dependent on ecosystem context.

Where cats are sympatric with larger predators, it is important to consider how interference or exploitation competition might influence habitat use by cats. In Chicago, Gehrt *et al.* (2013) found that cats preferentially used urban habitat types and were rarely found in natural fragments where coyotes were common, which suggested that interspecific competition and/or predation from the larger coyote was having a strong influence on habitat use by cats. In Australia, Molsher (1999) found that cats increased their use of open grasslands after the density of foxes using those areas was reduced, and Brook *et al.* (2012) found that cats were active earlier in the night at sites where dingoes were subject to lethal control compared to sites without lethal control. High levels of dietary overlap between sympatric carnivores may indicate resource competition, which can lead to interspecific aggression, including intra-guild predation (Polis *et al.* 1989; Donadio & Buskirk 2006). Alternatively, competition may not exist if the prey base is large enough to be shared between the two predators (Polis *et al.* 1989). Documenting the degree of overlap in diet and habitat use is a useful first step in determining whether resource competition may exist between sympatric carnivores.

Because cats are mobile, opportunistic predators, the distribution and habitat requirements of their prey also play an important role in structuring their habitat use (Fitzgerald & Turner 2000). In addition to evidence that cats focus their activity on areas with high prey abundance (Recio & Seddon 2013; Recio *et al.* 2014), habitat structure can also influence cat hunting success, and hence prey availability (McGregor *et al.* 2014) because cats rely heavily on sight and sound when hunting and use a mixture of cover and open areas to stalk and ambush their prey (Bradshaw 1992). The degree to which factors like predation, resource availability and vegetation structure influence cat habitat use varies according to local landscape conditions (Chapter 2), so local knowledge of cat habitat use is key to successful management programmes.

In this chapter, I use field studies in the semi-arid northern Wheatbelt region of Western Australia to examine habitat selection by cats with regard to the fire history of shrublands and the potential factors driving this (*Objective 2*) and

investigate overlap in resource use between sympatric cats and dingoes (*Objective 3*). I used remote cameras to examine patterns of habitat use by the two predators and pitfall trapping and sand pad data to examine spatial patterns in the activity of small mammals, reptiles and rabbits that cats prey on, as do dingoes to a lesser degree. Finally, I used scat analyses to describe the predators' diets and measure dietary overlap. I did not perform any formal analyses on the diet and habitat use of foxes because they were rarely recorded throughout the study.

Methods

Study area

I conducted this study in the northern Wheatbelt region of Western Australia ($29^{\circ} 38' S$, $117^{\circ} 08' E$), 400 km north-east of Perth. This area is situated between cleared agricultural land to the south and intact rangelands to the north and is bisected by the 1,170 km State Barrier Fence, which was built to exclude dingoes from agricultural land in the southwest of the state (Figure 3.1). Most of the study area is managed for conservation by Bush Heritage Australia (Charles Darwin Reserve) and the Australian Wildlife Conservancy (Mt Gibson Wildlife Sanctuary), and other land uses in the region include mining, pastoralism and Unallocated Crown Land. Further details of the study area can be found in Chapter 1.

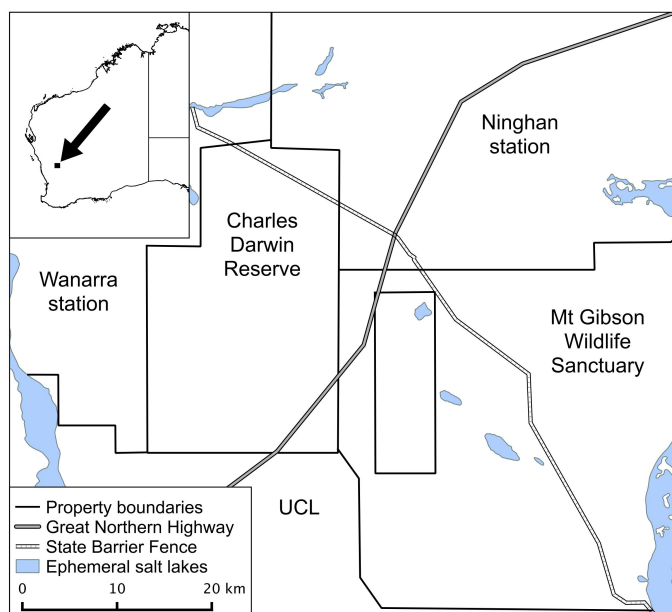


Figure 3.1 Location of the study area in Western Australia's northern Wheatbelt. The area nested within Mt Gibson Wildlife Sanctuary is managed for mining. UCL, Unallocated Crown Land.

Scat collection and analysis

I opportunistically collected predator scats along unsealed roads in the broader study area between March 2013 and September 2014. Scats were attributed to cats, foxes or dingoes in the field based on their size, shape, colour and odour (Triggs 2004). Any scats that could not confidently be assigned to a species were discarded. Scats were stored in individual paper bags and labelled with their collection location, date and species. I made no attempt to age scats because they are likely to desiccate quickly in the study area, hence precluding accurate estimates of age.

I sent all scats to a specialist (G. Story, <http://www.scatsabout.com.au/>) for analysis, who crosschecked and confirmed their assignment to predator species. Scats were dried in a 100°C oven for 12 hours to kill parasites. After drying, the samples were placed in individual fine-weave nylon bags and washed in a washing machine for approximately 15 minutes, leaving only indigestible items (hair, teeth, bones, skin, scales, feathers, plant material and arthropod exoskeletons). Prey remains were identified to the lowest possible taxonomic level by comparison of remains with known reference material or the literature (Watts & Aslin 1981; Brunner & Triggs 2002) and hair was identified using the technique described by Brunner and Coman (1974). Typically, mammalian prey remains were identified to species, reptiles to family, birds to class, and arthropods to class. Prey items were recorded for each scat and a percentage volume of each prey item within the scat was visually estimated using a grid system within the sorting tray.

Predator monitoring

I surveyed predator activity at Charles Darwin Reserve using 40 remote cameras (20 Moultrie i60 and 20 Scoutguard 560PV) each separated by a minimum distance of 2 km and positioned on vehicle tracks in a northern circuit and southern circuit (Figure 3.2). Cameras were fixed to a steel post so that the sensor was ~30 cm above the ground and were programmed to take a series of three photographs each time the sensor was triggered, with a minimum delay of one minute between triggers because this was the minimum possible delay for the Moultrie cameras. At half of the cameras, a raw chicken wing encased in a PVC bait holder pegged to the ground was used as a scent lure and at the remaining cameras an electronic device that makes the sound of a bird tweeting was used as

an audio lure (Lucky Duck, Wisconsin, USA). Audio and scent lures were swapped between cameras half way through each monitoring session such that each camera received equal exposure to the two lure types during each session. A fresh chicken wing was placed inside the bait holder each time the lures were swapped.

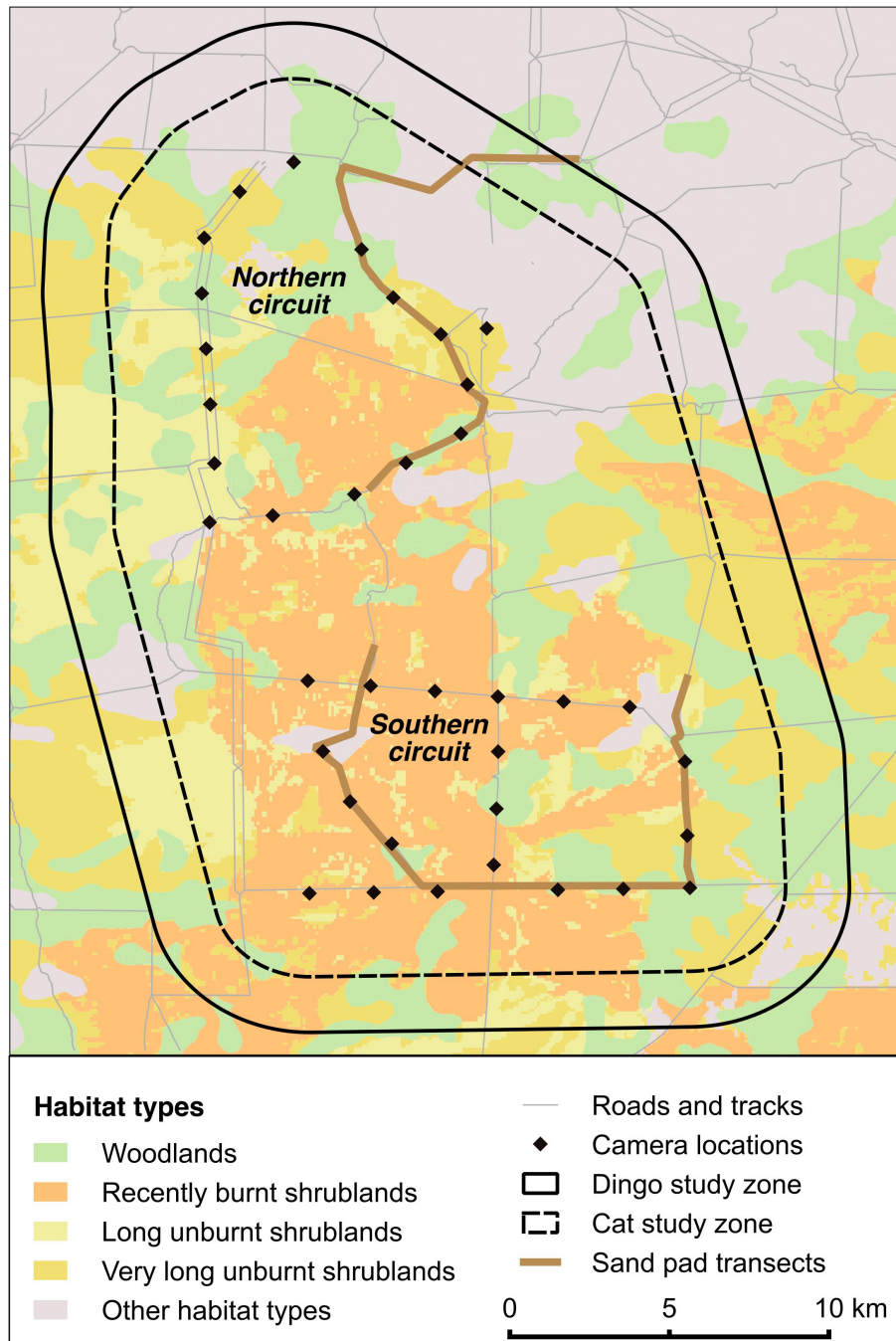


Figure 3.2 Distribution of habitat types and location of the remote cameras and sand pad transects. The locations of cameras N5, N19 and N20 are not shown on the map because they were excluded from analyses.

Cameras were activated for between two and five weeks in six monitoring periods: February, May, August and October 2013, and April and May 2014 (Table 3.1). Poison cat baits were laid in the southern part of the reserve in September 2013 and May 2014, and statistical analyses showed that the 2014 baiting led to a measurable decrease in cat activity, whereas the 2013 baiting did not (Appendix D). So to prevent potential changes in predator abundance influencing perceptions of their habitat use, I excluded from all analyses the data from the May 2014 session that followed the baiting event. At the end of each monitoring session, memory cards and lures were removed from camera sites and the cameras were deactivated. No data were available for cameras S7 and S19 in August 2013 because the cameras were stolen, nor was any data available for cameras N13 and S4 in February and October 2013 respectively because the cameras malfunctioned.

Table 3.1 Survey periods for remote cameras, pitfall trapping and sand pad monitoring. Grey boxes indicate monitoring periods for which the data was excluded from the analyses in this chapter.

Survey year and month	Cameras	Pitfalls ^A (RB/LU/W)	Sand pads
2010 Oct		6/6/4	
2011 Apr		6/6/4	
Oct		6/6/2	
2012 Oct		6/6/0	
Dec / Jan			3-4 days
2013 Feb	2 weeks		
April		6/6/0	
May	4 weeks		
Aug	5 weeks		
Sept 8 th	Baits laid		
Oct	5 weeks	8/8/4	
Dec / Jan			5 days
2014 Apr	5 weeks		4 days
May 11 th	Baits laid		
May	4 weeks		
July			4 days

^A Number of pitfall trapping sites in each of three habitat types: RB, recently burnt shrubland; LU, long unburnt shrubland; W, *Eucalyptus* woodland.

The remote camera methods were originally designed to measure the response of cats to a poison baiting programme (Appendix D), rather than to explicitly measure their habitat use, which is what the GPS collars were intended for (Appendix C). For this reason, some aspects of the camera methodology are not ideal for measuring habitat use. Ideally, cameras would have been deployed on a rolling basis at a great number of sites to better sample the range of habitat types at the reserve. Also, passive camera stations could have been used to prevent lures from potentially attracting animals to areas outside of their normal range. Additionally, surveys of prey abundance only partially overlapped with the camera surveys in both space and time. Nevertheless, this does not preclude useful information being gained from this study and I discuss the implications of these limitations throughout.

Prey monitoring

I used pitfall trapping data from the study site to determine whether there were differences in the abundance of small mammals and reptiles between three habitat types: recently burnt shrublands, long unburnt shrublands, and eucalypt woodlands (see *Habitat classification*). Specific details of the trapping methods can be found in Chapter 4. Pitfall trapping was undertaken at 16 or 20 sites in every October between 2010 and 2013 inclusive, as well April 2011 and 2013 (Table 3.1). The eucalypt woodlands were not surveyed in October 2012 and April 2013, so I excluded those periods from the analyses.

I examined the activity of rabbits using data from 47 sand pad monitoring plots collected as part of a separate study. Each plot consisted of a $\sim 1.5 \times 3$ m area of raked sand spanning the width of a track. Plots were separated by at least 1 km each and were situated on a northern transect ($n = 25$) and a southern transect ($n = 22$; Figure 3.2). Sand pads were monitored for three to five days in December/January 2012/13 and 2013/14, and April and July 2014 (Table 3.1). Each plot was raked smooth on the first morning and then checked daily for the presence of rabbit sign, such as tracks or droppings. Data was recorded as the presence/absence of rabbits on each plot for each day and plots were raked smooth after checking each day.

Habitat classification

I used vegetation communities ('land systems' *sensu* Payne et al. 1997) and fire ages to classify 17 habitat types (Table 3.2). Fire history information was extracted from spatial data layers in ArcMap (ESRI 2012) that were drawn from satellite imagery and aerial photography of historical fire scars (Braun 2006). There were no fires at the study site between 2005 when the fire maps were drawn and the completion of this study in 2014. The most recent fires occurred between 2000 and 2004 inclusive, and the oldest mapped fire scar is dated 1969, which is a collection of fire scars visible on the earliest aerial photography available for the study site (1969) and represents a number of fires of similar age from around that time (Braun 2006). Any areas of vegetation on the 1969 aerial photography that did not look to have been recently burnt were classified as 'very long unburnt' and are considered to have remained unburnt for > 50 years.

Table 3.2 Descriptions of land systems and fire ages that were used to calculate habitat diversity at each camera site. Land systems information is based on Payne et al. (1997). Land systems that were not directly surveyed by the remote camera surveys are marked with an asterisk.

Land system name	Soil and vegetation description	Fire ages ^A (year last burnt)
Bandy*	Gritty-surfaced plains and low outcrops of granite with scattered acacia shrublands.	1, 3, 4
Bannar*	Level to gently undulating sandy plains with acacia shrublands, commonly with patchy native pines and mallees.	1, 2, 4
Carnegie*	Salt lakes with fringing saline alluvial plains, kopi dunes and sandy banks, supporting halophytic shrublands.	4
Challenge*	Gently undulating gritty-surfaced plains, occasional granite hills, tors and low breakaways, with acacia shrublands.	4
Euchre, Pindar	Low granite breakaways with alluvial or loamy plains, sandy tracts or sandplain supporting eucalypt woodlands and acacia shrublands.	All fire ages pooled
Joseph	Undulating yellow sandplain supporting dense mixed shrublands with patchy mallees.	1, 2*, 3, 4
Kalli*	Red sandplains supporting bowgada shrublands with wanderrie grasses.	4
Waguin*	Low breakaways with short stony and sandy plains, supporting acacia shrublands and minor halophytic shrublands.	4
Yowie*	Loamy plains supporting shrublands of mulga and bowgada with patchy wanderrie grasses.	4
Cleared* (human-use)	Highly modified vegetation, mostly cleared, such as paddocks and infrastructure. This classification is not from Payne et al. (1997).	N/A

^A 1, 10–14 years since last fire (YSLF); 2, 19–29 YSLF; 3, 34–49 YSLF; 4, > 50 YSLF.

For the analyses that follow, I defined the area of interest (herein 'cat/dingo study zone') as a maximum convex polygon around the peripheral camera locations with a 3 km buffer for cats and a 5 km buffer for dingoes (Figure 3.2). The buffers were chosen to capture areas of habitat that lay beyond the edges of the camera array, but were still potentially available to animals recorded on the cameras. A radius of 3 km equates to a circle of $\sim 28 \text{ km}^2$ and was chosen because mean cat home range estimates from similar environments in Australia range from 2.48 to 22.1 km^2 (Jones & Coman 1982; Edwards et al. 2001; Molsher et al. 2005; Hilmer 2010; Bengsen et al. 2012). Similarly, a radius of 5 km equates to a circle of $\sim 79 \text{ km}^2$ and mean dingo home range estimates from similar environments range from 24 to 77.3 km^2 (Thomson 1992a; Allen 2012; Allen et al. 2014).

I calculated habitat diversity within a 500-m radius around each camera site using Shannon's Diversity Index. I did not assess habitat use at larger scales because remote cameras represent static points and hence are not necessarily representative of broader home ranges. Within the same radii, I also calculated the proportion of four primary habitat types that collectively account for $\geq 80\%$ of both the cat and dingo study zones. These were: (i) *Eucalyptus* woodlands (Pindar and Euchre land systems); (ii) 'recently burnt' Joseph land system shrublands (10 to 14 years since last fire), (iii) 'long unburnt' Joseph shrublands (34 to ~ 49 years); and (iv) 'very long unburnt' Joseph shrublands (> 50 years). These fire age classifications are based on previous work at the study site (Knuckey & van Etten 2012; Dalgleish et al. 2015). I did not classify the eucalypt woodlands according to fire ages because the woodlands generally only burn at the edges and hence the large majority of these areas are unburnt. The eucalyptus woodlands are open stands of mostly *Eucalyptus loxophleba* trees, with scattered shrubs and a sparse understorey. The shrublands are situated on sandplains, with the recently burnt areas lacking a distinct canopy and containing a single homogenous layer of vegetation between 0 and 2 m above the ground (Parsons & Gosper 2011; Dalgleish et al. 2015). The long unburnt shrublands are characterised by variable structure between 0 and 4 m, although the most dense vegetation is between 0 and 2 m, whereas the very long unburnt shrublands are more open in the 0 to 2 m stratum and more dense between 2 and 4 m, and also exhibit greater patch size variability (Dalgleish et al. 2015). Using these habitat types, I classified each

camera location according to the dominant habitat within 500-m of each camera. In all cases where there were multiple habitat types around a camera, the dominant habitat was also the one overlaying the precise camera location. I excluded three cameras (N5, N19, N20) that were located in habitat types represented by one and two cameras each. Of the 37 remaining cameras, 10 were located in woodlands, 15 in recently burnt shrublands, four in long unburnt shrublands and eight in very long unburnt shrublands.

Statistical analysis

Dietary estimates

Prey items were classified into the following categories: small mammals (< 500 g), medium-sized mammals (500–6,999 g), large mammals ($\geq 7,000$ g), reptiles, birds, arthropods and vegetation. Mammals were grouped based on maximum body weights listed in Van Dyck et al. (2013) and the size ranges of Glen and Dickman (2006). Given their large body size relative to cats, the presence of large mammal remains in cat scats was assumed to represent consumption of carrion. For individual prey items and prey groups, I calculated the percentage frequency of occurrence (%*F*: percentage of scats containing a certain type of food). I also calculated the percentage volume of prey types in scats (%*V*: the volume of a certain type of food in the scats expressed as a percentage of the total volume of all food types in the scats). The %*F* may overestimate the importance of small food items that occur frequently, whereas the %*V* may underestimate consumption of items that are easily digested. It is therefore recommended that dietary studies use both metrics (Glen & Dickman 2006; Klare et al. 2011).

To assess whether the sample sizes were adequate to describe predator diets, I calculated cumulative diversity using the Brillouin index (Brillouin 1956). I also calculated Herrera's trophic diversity index (*D*), which is appropriate for presence-absence diet data, whereas other measures such as the Shannon or Levin's index are not (Herrera 1976). The index equals 0 when all food groups are found in all samples, and increases as food groups are eaten less evenly relative to each other. I used Pianka's index (*O*) to calculate the degree of dietary overlap between predator species (Pianka 1973). The index ranges from 0 (no food groups in common) to 1 (all food groups consumed with identical frequency).

Camera data

Remote camera images were stored in a database and tagged with the camera identification number, circuit (north or south), session, date, time and species using EXIFPro 2.0 (Kowalski & Kowalski 2012). Tags were written to the EXIF data of each file and then exported from EXIFPro as a text file. To ensure independence of repeat photographs of the same species caught on the same camera, I classified photographs that were captured within 15 minutes of each other as a single photo 'event'. Inspection of frequency tables of the time elapsed between photographs indicated that this was a suitable breakpoint (Table 3.3). For each session, I summed the total number of independent photo events of each species at each camera.

Table 3.3 Percentage of photo events for cats and dingoes within time brackets between successive photos on the same camera within each session.

Time bracket (mins)	Cat	Dingo
0 to 15	80.29%	81.51%
16 to 30	0.00%	0.68%
31 to 100	0.36%	1.37%
101 to 500	2.92%	3.42%
500 to 40,000	16.42%	13.01%

Predator activity

To identify spatial patterns in predator activity, I calculated activity indices (AI) by dividing the total number of independent photos across all periods by the total number of camera-nights and multiplied this by 100, to give the number of photos per 100 camera-nights. I then plotted these values on a map of the study site using a colour gradient of increasing predator activity. To investigate temporal patterns in diurnal predator activity, I plotted circular histograms showing the frequency of photo events for cats and dingoes occurring during each hour of the day and night. I also calculated mean daily activity times using the `circadian.mean` function in the `psych` package in R (Revelle 2014). Although I did consider examining potential temporal segregation between cats and dingoes, the very small sample size for the number of cameras that recorded both cats and dingoes within the same session ($n = 9$) precluded any meaningful analysis being done.

Habitat use

I used Poisson generalised linear mixed models (GLMMs) to test the effect of habitat types on predator activity. I used the number of independent photograph events per camera in each session as the response variable and used the number of nights cameras were active ('camera-nights') as an offset to account for variable sampling effort. I fitted single term models of cat and dingo activity with each of the habitat predictor variables (habitat diversity and proportion of the four habitat types) and included camera ID, model (Moultrie or Scoutguard) and session as random intercepts. I calculated 95% confidence intervals (*CI*) for each predictor variable and inferred 'significant' effects where the confidence intervals did not overlap zero. The five predictor variables were not strongly correlated (Pearson's $r < \pm 0.5$ in all cases). To determine whether there was a spatial relationship between cat and dingo activity, I also modelled cat activity as a function of the dingo activity index.

Habitat selection

Given that some habitat types cover proportionally larger areas than others, it was also important to assess habitat use relative to availability. To do this, I calculated habitat selection ratios using a type I design (*sensu* Thomas & Taylor 1990), i.e. individual animals were not identified and habitat selection was measured at the population level. Selection ratios (w_j) > 1 indicate habitat preference and values < 1 indicate habitat avoidance (Manly et al. 2002), and are calculated using the formula:

$$w_j = \frac{u_j}{a_j}$$

where u_j is the proportional use of habitat type j and a_j is the proportional availability of habitat type j (Manly et al. 2002). Because of the limitations in the sampling design, the camera locations represented only a subset of the possible habitat types at the reserve, albeit the most common (the four major habitat types collectively cover 84% of the cat study zone and 80% of the dingo study zone). For this reason, I only included these four habitat types in the calculation of habitat selection ratios. Habitat use (u_j) was calculated as a standardised activity index for each camera, which was summed and converted to a percentage for each of the four habitat types that the cameras were classified as belonging to. Habitat

availability (a_j) was calculated as the proportion of each habitat type within the study zone boundaries. I pooled data from all sessions to calculate overall habitat selection ratios for cats and dingoes, and also examined any seasonal changes by calculating selection ratios for each of the five monitoring sessions for cats only. I did not calculate seasonal selection ratios for dingoes because they were recorded relatively infrequently (14 out of 181 possible camera \times session combinations), hence the small sample sizes precluded any meaningful inferences being made. Significance of habitat selection ratios was tested using chi-squared goodness of fit statistics in the R package *adehabitatHS* (Calenge 2006). Significance of the main test was inferred at $\alpha = 0.05$ and preferential use or avoidance of each habitat type was assessed using a Bonferroni-corrected alpha level of 0.0125.

Prey abundance

I used GLMMs assuming a normal error distribution to test the effect of habitat type (three levels) on small mammal abundance, reptile abundance and total abundance of both groups. For each trapping session, I summed the total number of reptiles and mammals captured at each trapping site. To account for variable sampling effort, I standardised these values to the number of animals captured per 100 trap-nights. I included trapping period and site as random intercepts to account for repeat sampling of sites over time. I used $\alpha = 0.05$ to determine the significance of habitat type and if significant, I made pairwise comparisons between habitat types using Tukey contrasts.

For the sand pad data, I calculated an index of rabbit activity by dividing the number of days each plot recorded rabbit sign by the number of survey days during each period and multiplied this by 100, to give the number of plots with rabbit activity per 100 nights. To identify spatial patterns in rabbit activity, I averaged plot values across all monitoring sessions and plotted them on a map of the study site using a colour gradient of increasing rabbit activity. I also performed a *t*-test on mean rabbit activity for the northern and southern transects. Both the sand pad and pitfall trapping data were used to make comparisons of prey abundance/activity amongst habitat types or locations, rather than to be used as strict predictors of predator activity. All analyses were done in R version 3.0.2 (R Core Team 2013).

Results

Diet

I collected 123 cat, 37 dingo and three fox scats between March 2013 and September 2014. The Brillouin index of diet diversity reached an asymptote at a sample size of around 20 scats for cats, and around 15 scats for dingoes (Figure 3.3). Rabbit was the highest ranked food item for cats in terms of both frequency (59%) and volume (43%), followed by reptiles, small mammals and birds (Table 3.4, Figure 3.4). Cat scats contained rodent remains more frequently than those of dasyurids, and contained the remains of skinks and varanids more frequently than those of dragons and snakes (Table 3.4). Arthropods such as grasshoppers, crickets, centipedes, scorpions, spiders, ants and termites were found in 42% of cat scats, but contributed little to their volume (3.6%) (Table 3.4). Few cat scats contained the remains of large mammals (6%), whereas this group was found in 62% of dingo scats. Rabbit remains were the second most frequently occurring food item in dingo scats (22%), followed by bird remains (16%). Dingo scats did not contain small mammal remains and infrequently contained arthropod and reptile remains (Table 3.4). Dietary overlap (O) between dingoes and feral cats was 0.45. Dietary diversity (D) of feral cats (6.20) was higher than that of dingoes (5.09).

The mammal species eaten by cats in order of decreasing % F were: rabbits, Mitchell's hopping mouse *Notomys mitchellii*, house mouse *Mus musculus*, sandy inland mouse *Pseudomys hermannsburgensis*, dunnart *Sminthopsis* sp., little long-tailed dunnart *Sminthopsis dolichura*, red kangaroo *Macropus rufus* (assumed to be carrion), indeterminate rodent, euro *Macropus robustus* (assumed to be carrion), cat (as prey), Gilbert's dunnart *Sminthopsis gilberti*, spinifex hopping mouse *Notomys alexis* and a microbat (possibly *Nyctophilus* sp.) (Table 3.4). For dingoes, the species were: red kangaroo, euro, rabbit, echidna *Tachyglossus aculeatus*, dingo (as prey), *Macropus* sp. and goat *Capra hircus* (Table 3.4). Three mammal species were recorded in fox scats: little long-tailed dunnart, Mitchell's hopping mouse and *Macropus* sp.

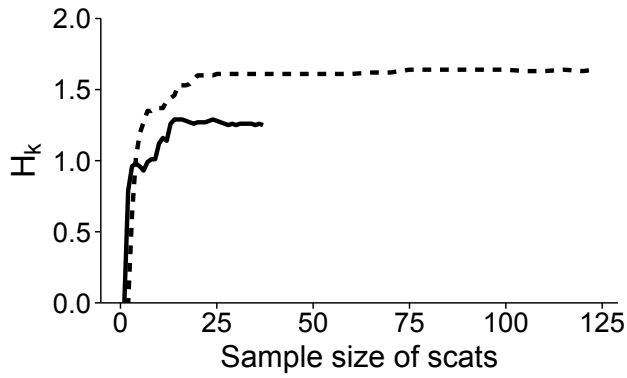


Figure 3.3 Cumulative diversity (H_k) of cat (dashed line) and dingo (solid line) diet with increasing sample size of scats.

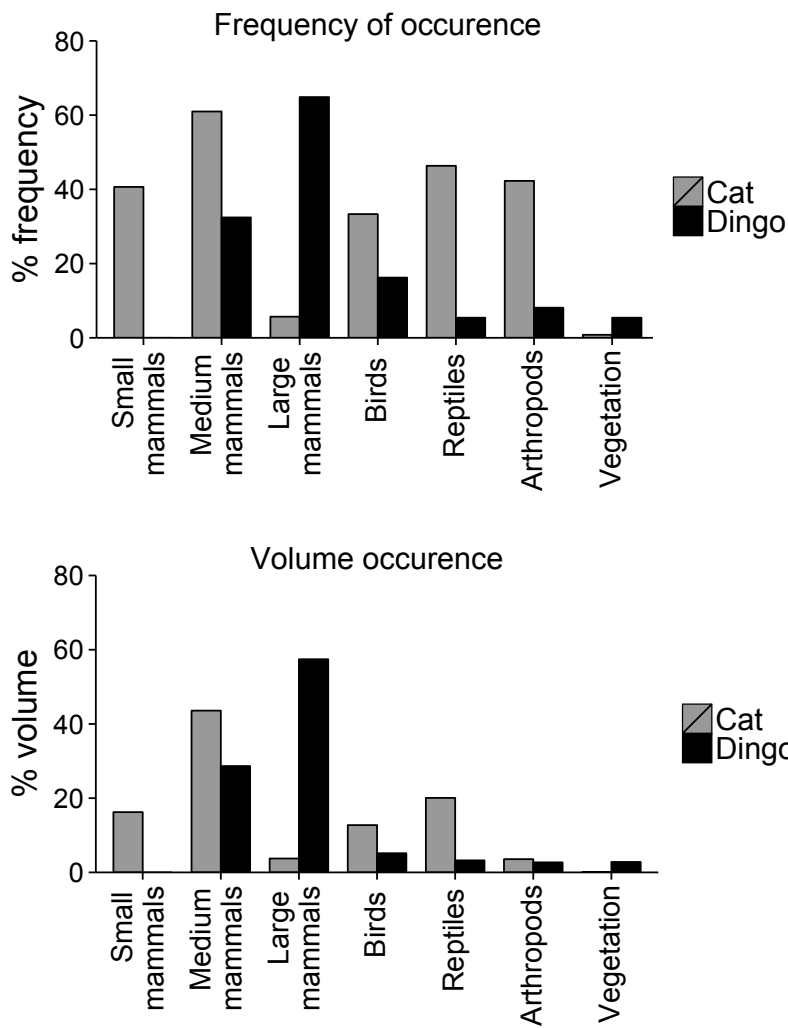


Figure 3.4 Frequency of occurrence (%F) and volume occurrence (%V) of food groups in feral cat and dingo scats.

Table 3.4 Occurrence of prey species and food groups in feral cat, dingo and fox scats. %F, percentage frequency of occurrence; %V, percentage occurrence by volume.

Food item	Cat (n = 123)		Dingo (n = 37)		Fox (n = 3)	
	%F	%V	%F	%V	%F	%V
<i>Sminthopsis dolichura</i>	4.1	2.0	0	0	33.3	10.0
<i>Sminthopsis gilberti</i>	0.8	0.4	0	0	0	0
<i>Sminthopsis</i> sp.	4.9	0.8	0	0	0	0
Total dasyurids	9.8	3.2	0	0	33.3	10.0
<i>Mus musculus</i>	13.0	4.2	0	0	0	0
<i>Notomys alexis</i>	0.8	0.1	0	0	0	0
<i>Notomys mitchellii</i>	16.3	7.1	0	0	33.3	31.7
<i>Pseudomys hermannsburgensis</i>	4.9	1.3	0	0	0	0
Rodent indeterminate	1.6	< 0.1	0	0	0	0
Total rodents	35.0	12.7	0	0	33.3	31.7
Microbat, possibly <i>Nyctophilus</i> sp.	0.8	0.3	0	0	0	0
Total small mammals (< 500 g)	40.7	16.2	0	0	66.7	41.7
Rabbit <i>Orcytolagus cuniculus</i>	59.3	43.3	21.6	18.8	0	0
Echidna <i>Tachyglossus aculeatus</i>	0	0	10.8	9.9	0	0
Cat <i>Felis catus</i>	1.6	0.3	0	0	0	0
Total medium-sized mammals (500 – 6999 g)	61.0	43.6	32.4	28.6	0	0
<i>Macropus robustus</i>	1.6	1.1	27.0	23.5	0	0
<i>Macropus rufus</i>	4.1	2.7	27.0	23.9	0	0
<i>Macropus</i> sp.	0	0	2.7	< 0.1	33.3	33.3
Total macropods	5.7	3.7	56.8	47.5	0	0
Dingo <i>Canis lupus dingo</i>	0	0	8.1	7.3	0	0
Goat <i>Capra hircus</i>	0	0	2.7	2.7	0	0
Total large mammals (≥ 7000 g)	5.7	3.7	62.2	57.4	33.3	33.3
Emu <i>Dromaius novaehollandiae</i>	0	0	2.7	1.4	0	0
Bird	33.3	12.7	13.5	3.8	0	0
Total birds	33.3	12.7	16.2	5.2	0	0
Geckoes	0	0	0	0	0	0
Skinks	39.8	8.9	2.7	0.5	33.3	6.7
Dragons	4.1	1.5	0	0	0	0
Varanids	20.3	9.6	2.7	2.7	0	0
Snakes	0.8	< 0.1	0	0	0	0
Total reptiles	46.3	20.1	5.4	3.2	33.3	6.7
Beetle/cockroach	30.1	1.7	8.1	1.4	33.3	1.7
Grasshopper/cricket	13.0	1.0	0	0	0	0
Caterpillar	0	0	2.7	1.1	0	0
Centipede	4.9	0.6	0	0	33.3	16.7
Scorpion	0.8	0.1	0	0	0	0
Spider	1.6	0.1	2.7	0.3	0	0
Ants/termites	7.3	0.2	0	0	0	0
Total arthropods	42.3	3.6	8.1	2.7	66.7	18.3
Vegetation	0.8	< 0.1	5.4	2.8	0	0

Camera data

The cameras captured 95 independent photos of feral cats, 29 of dingoes and three of foxes during 4,675 camera-nights (excluding May 2014 and cameras N5, N19 and N20). Cameras also recorded images of rabbits, kangaroos, dunnarts, Mitchell's hopping mouse, goannas *Varanus* spp., dragons *Ctenophorus* spp., the western bluetongue skink *Tiliqua occipitalis*, emus *Dromaius novaehollandiae*, malleefowl *Leipoa ocellata*, butcherbirds *Cracticus* spp., raptors and small passerine birds.

Predator activity

Across the study, 90% of the northern cameras recorded cats, which accounted for 72.4% of all cat detections, whilst only 65% of the southern cameras recorded cats (27.6% of detections) (Figure 3.5). Similarly, dingoes were recorded on 50% of the northern cameras, which accounted for 93.3% of detections, whereas dingoes were only recorded on three occasions and 10% of cameras on the southern circuit (6.7% of detections) (Figure 3.5). Accordingly, activity indices for cats and dingoes on the northern circuit were higher than the southern (Figure 3.5).

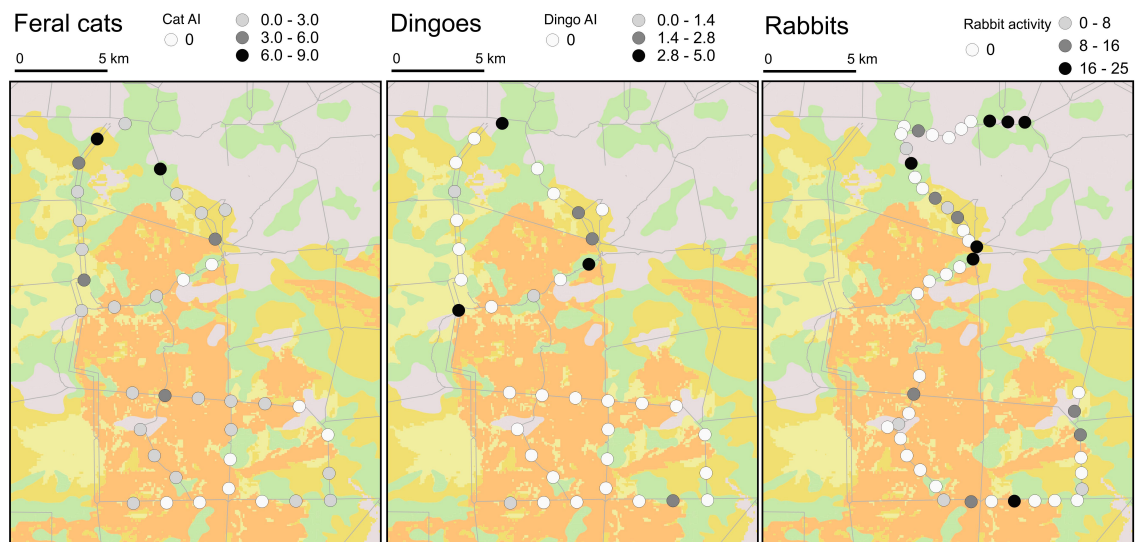


Figure 3.5 Spatial intensity of feral cat, dingo and rabbit activity. Darker circles represent higher activity, and white circles represent sites where cats, dingoes or rabbits were never recorded. Cat and dingo AI: number of photos per 100 camera-nights for the entire study period, excluding May 2014. Rabbit activity: number of plots with rabbit activity per 100 nights.

Of the 28 cameras that recorded cats at any time during the study, eight recorded cats in three, four or five sessions, nine in two sessions, and 11 in one session only. Of the 65 combinations of camera × session that recorded at least cats or dingoes throughout the study, 78.5% recorded cats only, 12.3% recorded dingoes only, and 9.2% recorded both cats and dingoes. Mean time of activity for feral cats was 11:35 pm, with 78% of cat photo events occurring between 6pm and 6am (Figure 3.6). Mean time of activity for dingoes was 09:02 pm, with 68% of dingo photo events occurring between 4pm and 4am (Figure 3.6).

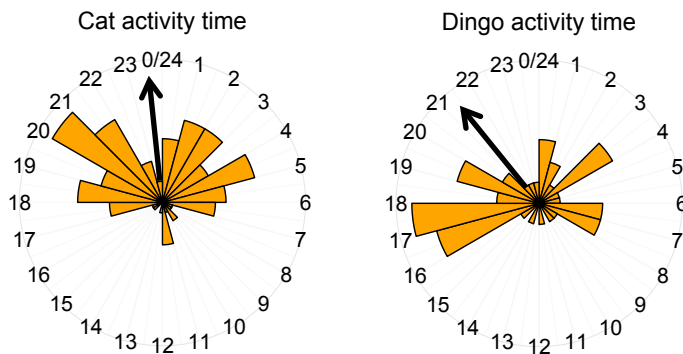


Figure 3.6 Frequency of photo events during each hour of the day and night for feral cats and dingoes. The black arrows indicate approximate mean activity time.

Habitat use

Of the 95 cat photo events, 38.95% were recorded in very long unburnt shrublands, 28.42% in recently burnt shrublands, 20% in woodlands and 12.63% in long unburnt shrublands. Of the 29 dingo photo events, 48.28% were recorded in woodlands, 24.14% in very long unburnt shrublands, 17.24% in long unburnt shrublands and 10.34% in recently burnt shrublands. The mixed modelling results showed that cat activity was negatively correlated with the amount of recently burnt shrublands within 500-m of camera sites, and positively correlated with the amount of very long unburnt shrublands within 500-m of camera sites (Table 3.5). There was no relationship between cat activity and the other habitat variables, cat and dingo activity, or dingo activity with any habitat variables (Table 3.5).

Table 3.5 Mixed modelling results for the effect of habitat variables on cat and dingo activity, and dingo activity on cat activity. * significant at 0.05

Variable	Feral cat activity		Dingo activity	
	Model estimate	95% CI	Model estimate	95% CI
Woodlands	-0.27	-1.37, 0.72	1.94	-2.36, 6.66
Recently burnt shrublands	* -0.92	-1.77, -0.11	-2.56	-6.76, 1.03
Long unburnt shrublands	0.79	-0.66, 2.35	-0.14	-10.00, 7.47
Very long unburnt shrublands	* 1.11	0.27, 2.03	0.64	-4.75, 5.56
Shannon diversity	-0.70	-1.58, 0.16	1.35	-2.57, 5.28
Dingo activity	0.06	-0.01, 0.11	-	-

Habitat selection

The overall test of habitat selection by cats was significant for all sessions combined ($\chi^2(3) = 19.16, P < 0.001$), as well as February 2013 ($\chi^2(3) = 71.81, P < 0.001$), August 2013 ($\chi^2(3) = 109.80, P < 0.001$), October 2013 ($\chi^2(3) = 65.61, P < 0.001$) and April 2014 ($\chi^2(3) = 38.27, P < 0.001$), but not May 2013 ($\chi^2(3) = 5.57, P = 0.135$). The overall test of habitat selection by dingoes was significant ($\chi^2(3) = 24.59, P < 0.001$). For all sessions combined, cats showed a significant preference for very long unburnt shrublands, whereas dingoes showed a significant preference for woodlands and avoidance of recently burnt shrublands (Table 3.6). In the first session, cats showed a significant preference for recently burnt shrublands and significant avoidance of woodlands and long unburnt shrublands. Whereas in the third, fourth and fifth sessions, cats showed a significant avoidance of recently burnt shrublands and a significant preference for very long unburnt shrublands (Table 3.6). In the third and fourth sessions, cats also showed a significant avoidance of long unburnt shrublands and woodlands respectively (Table 3.6). Cats did not exhibit significant preference or avoidance of any habitat type in the second session (Table 3.6).

Table 3.6 Habitat selection ratios (w_j) for cats and dingoes across all sessions, and cats in individual sessions. Values > 1 indicate preference for a habitat type, and values < 1 indicate avoidance. Significance (*) was inferred using a Bonferroni level of $P < 0.0125$.

Habitat type	Dingo	Cat	Session ^A				
	Total	Total	(1)	(2)	(3)	(4)	(5)
Woodlands	1.59*	0.70	0.30*	0.68	1.32	0.41*	0.92
Recently burnt shrublands	0.40*	0.80	1.88*	1.00	0.22*	0.47*	0.44*
Long unburnt shrublands	1.12	0.85	0.00*	1.29	0.00*	1.30	1.00
Very long unburnt shrublands	1.00	1.99*	1.01	1.25	2.88*	2.73*	2.28*

^A Session (1): Feb. 2013, (2) May 2013, (3) August 2013, (4) Oct. 2013, (5) April 2014

Prey abundance

Small mammal abundance was significantly different between habitat types ($\chi^2(2) = 13.31, P = 0.001$), with recently burnt shrubland sites having higher small mammal abundance than both woodland ($P = 0.002$) and long unburnt shrubland sites ($P = 0.017$; Figure 3.7). Reptile abundance ($\chi^2(2) = 8.85, P = 0.012$) and total abundance ($\chi^2(2) = 8.95, P = 0.011$) were also significantly different between habitat types (Figure 3.7). In both cases, woodland sites had lower values than both recently burnt (reptiles $P = 0.031$; total $P = 0.014$) and long unburnt shrubland sites (reptiles $P = 0.012$; total $P = 0.020$). Rabbit activity on the northern transect (mean \pm SE: 6.33 ± 1.71 plot intrusions per 100 nights) was higher than the southern transect (3.81 ± 1.23), although the difference was not significant ($t_{42.4} = 1.20, P = 0.237$). Rabbits were recorded on 44% of sand pads in the north and 36% in the south (Figure 3.5).

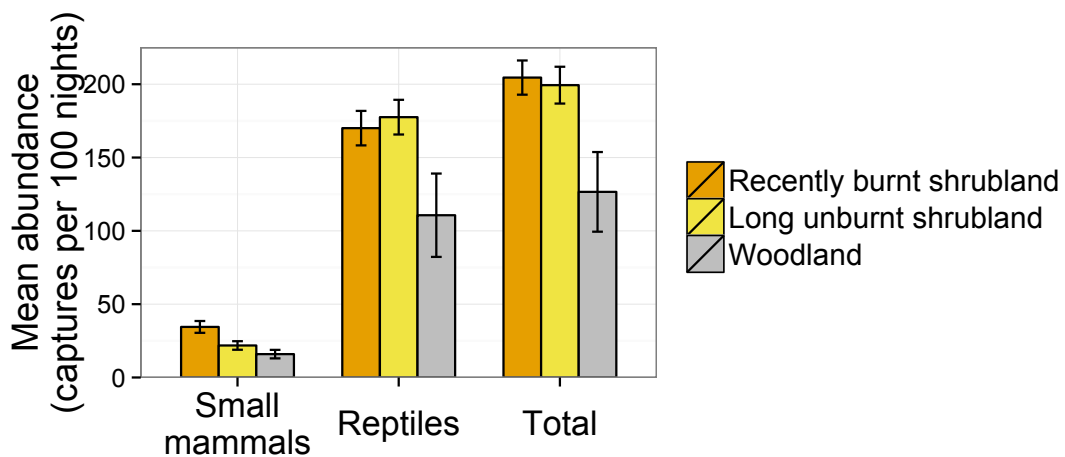


Figure 3.7 Means and standard errors of small mammal, reptile and total abundance in three habitat types: recently burnt shrublands, long unburnt shrublands and woodlands.

Discussion

Prey availability as a driver of habitat selection by cats

Given that predator-prey habitat selection models and optimal foraging theory predict that the distribution of food resources should influence predator habitat use (Pyke 1984; Mitchell & Powell 2004; Börger et al. 2008), prey availability may help explain the observed patterns of cat habitat selection. The preference by feral cats for very long unburnt shrublands may be influenced by the high small mammal and reptile abundance recorded in the long unburnt shrublands, which is the habitat type most structurally-similar to the very long unburnt shrublands. Although, prey abundance there was similar to the recently burnt shrublands which cats were recorded in less frequently. The dietary analysis showed that cats feed on both small mammals and reptiles in the study area, although the abundance of these two groups may not be a strong determinant of cat habitat use in the study landscape and/or during the study period, especially since rabbits occurred in cat scats more frequently and in greater volume. Like cat activity, rabbit activity was generally higher in the north of the reserve than in the south. Cats may be concentrating their activity in the northern part of the reserve to exploit a key prey resource (Recio & Seddon 2013; Recio et al. 2014). Also, cats may be attracted to rabbit warrens which they are known to shelter in (Read & Bowen 2001).

It is important to note that cat activity on the southern circuit was similar to the northern in the first two monitoring sessions, but declined to lower levels for the remaining sessions (see Appendix D), hence resulting in seasonal differences in the habitat selection ratios. For example, in the first session when cat activity on the southern circuit was highest, cats showed a significant preference for recently burnt shrublands, whereas they showed a significant avoidance of that habitat type in three out of the four sessions that followed. A possible explanation for this pattern is seasonal changes in prey availability, i.e. we may expect that cats would move out of an area if seasonal prey availability decreased (Pierce et al. 1999); however, little is known about potential seasonal changes in rabbit or small mammal abundance between different habitat types or parts of the reserve. The decline occurred from late summer through autumn and winter, which coincides with seasons of lower daily maximum temperatures and hence lower reptile

activity, but there is no obvious reason why this phenomenon would be restricted to areas dominated by recently burnt shrublands. In fact, recently burnt shrublands are more open and lack a distinct canopy compared to older shrublands and hence should provide reptiles with better thermoregulatory opportunities than older shrublands. The reason for this decline remains unclear, although it occurred after I trapped and fitted GPS collars to 14 cats in March 2013, most of them in that same general area (Appendix C). The possibility that the cats left this area in response to capture and handling may be responsible for their apparent preference for very long unburnt shrublands.

Habitat structure can also influence prey availability for carnivores. Rather than selecting areas with high absolute prey abundance, some carnivore species select habitats with high prey 'catchability' (Hopcraft et al. 2005; Rajaratnam et al. 2007). The negative relationship between cat activity and the amount of young shrubland at a site may be related to the homogenous structure of this habitat type. Since cats rely heavily on sight and sound when hunting and use a mixture of cover and open areas to stalk and ambush their prey (Bradshaw 1992), I hypothesised in Chapter 2 that dense homogeneous habitats should be unfavourable areas for hunting by cats. Previous studies have found that cats avoided similarly homogenous habitats, such as grasslands (McTier 2000; Edwards et al. 2002), agricultural land (Hall et al. 2000) and heather moorland (Daniels et al. 2001), although these patterns aren't universal. The recently burnt shrublands in this study lack a distinct canopy and contain a single homogenous layer of vegetation between 0 and 2 m above the ground (Parsons & Gosper 2011; Dalgleish et al. 2015). Older shrublands, on the other hand, are characterised by variable structure between 0 and 4 m above the ground and greater patch size variability (Parsons & Gosper 2011; Dalgleish et al. 2015). Structurally heterogeneous habitats, such as the very old shrublands here, may improve cat hunting success by providing a mixture of both cover and open areas in which they can observe, stalk and ambush their prey (Leyhausen 1979; Bradshaw 1992). Cat activity showed a positive relationship with the amount of very long unburnt shrublands at a camera site and these structurally-diverse areas may therefore facilitate cat hunting success by providing a mixture of open areas and cover.

Overlap in habitat use by cats and dingoes

Another possible explanation for the observed patterns relates to intra-guild predation and competition. In Chapter 2, I proposed that intra-guild species can have a strong influence on cat habitat use, especially where the other predator has a strong competitive ability and high dietary overlap with cats (Heithaus 2001; Wilson et al. 2010; Ross et al. 2012). Potential intra-guild competitors/predators in the study region are the dingo and the red fox, both of which are known to have temporally and spatially suppressive impacts on feral cats (Molsher 1999; Risbey et al. 2000; Moseby et al. 2012; Brook et al. 2012; Wang & Fisher 2013). Foxes were only recorded on three occasions throughout the study and hence are unlikely to have influenced cat habitat use. Although dingoes were more common, they were recorded relatively infrequently compared to cats, and cats were recorded at nearly half the sites where dingoes were also recorded during the same session. Given the low number of records for dingoes, it is difficult to make inferences about their possible influence on spatial patterns of habitat use by cats.

I did, however, find some support for differences in the daily activity times of cats and dingoes. Across all sessions and cameras, peak cat activity occurred two and a half hours later than peak dingo activity, although there was some overlap. This result concurs with a study from eastern Australia where feral cat activity also peaked later than dingo activity (Wang & Fisher 2013), and the finding of Brook et al. (2012) that cats were active earlier in the night at sites where dingoes were subject to lethal control compared to sites without lethal control. Given that dingoes will attack and kill cats (Moseby et al. 2012), feral cats in this study may be avoiding aggressive encounters with dingoes by being most active later in the night. The small sample sizes and variable dingo activity limit the strength of these conclusions, which could be explored further using manipulative experiments (e.g. Newsome et al. 2015).

Overlap in the diets of cats and dingoes

The diet of feral cats was more diverse than that of dingoes, with cats consuming 11 mammal species and dingoes six. Cats also consumed birds and reptiles much more frequently than dingoes and these two groups are likely to be comprised of several different species, although it is difficult to identify them to the species level from scat samples. Rabbits were the most common food item in feral

cat scats, which supports previous findings from similar parts of Western Australia (Martin et al. 1996; Risbey et al. 1999). Medium- and large-sized mammals, mostly rabbits and macropods, were the most frequently occurring food items in dingo scats and this also supports similar results from other semi-arid locations (Whitehouse 1977; Marsack & Campbell 1990; Thomson 1992b). The absence of small mammal remains in dingo scats may be an artefact of the small sample size, although previous studies from the rangelands have also recorded low frequencies of small mammals in dingo scats or stomachs (Whitehouse 1977; Marsack & Campbell 1990; Thomson 1992b), hence the absence of small mammal remains may be a true reflection of their diet.

The level of dietary overlap between cats and dingoes was relatively low ($O = 0.450$), however, few studies have compared the diet of sympatric cats and dingoes, with most similar studies making comparisons between foxes and cats (e.g. Catling 1988; Kirkwood et al. 2013), or foxes and dingoes (e.g. Glen et al. 2006; Cupples et al. 2011). Glen et al. (2011) recorded a similar level of overlap ($O = 0.496$) between wild dogs (dingoes and dog/dingo hybrids) and cats in eastern Australia and also found that small mammals were important prey for cats, whereas large mammals were more important for dogs. Dietary overlap in central Australia was higher ($O = 0.650$), mostly due to the high consumption of reptiles and birds by both species, although macropods were again important for dingoes and small mammals for cats (Paltridge 2002). In the current study, rabbit remains occurred relatively frequently in both cat and dingo scats, but small mammals, reptiles and birds were also common in cat scats, and macropods in dingo scats. This suggests that there may not be a high level of dietary competition between the two species at the study site during the study period. Although, dietary overlap and competition may vary across different years with changes in rainfall and hence prey availability. Additionally, if foxes were more common at the study site, higher levels of dietary overlap are likely to occur between cats and foxes, and foxes and dingoes (Paltridge 2002; Glen et al. 2011).

Study limitations

It is important to acknowledge the limitations of this study and how this might influence interpretation of the observed patterns. Firstly, as described in the methods, the remote camera surveys were not designed to capture the full suite of

habitat types at the reserve. The land systems not covered by the camera surveys were mostly concentrated in the north-eastern periphery of the study zones and, without having surveyed them, I am unable to comment on the relative activity of cats and dingoes in these areas. Although I am confident I have captured the major patterns in habitat use and selection because the unsurveyed habitat types covered only 16 and 20% of the cat and dingo study zones respectively. Additionally, remote cameras are not the ideal tool for assessing predator habitat use and interspecific competition because the activity indices derived from this method are difficult to validate (Hayward et al. 2015). Concurrent GPS-tracking of sympatric predators is a much more sound approach (e.g. Gehrt et al. 2013), although this was not possible here due to reasons outlined elsewhere.

Secondly, recently burnt shrublands were mostly concentrated in the south of the reserve, whereas the longer unburnt areas were mostly in the north. It is, therefore, difficult to determine whether the apparent preference by cats for the very long unburnt shrublands and the avoidance by dingoes of recently burnt shrublands were true representations of habitat selection, or rather were there some unmeasured factors driving higher cat and dingo activity in the north of the reserve and hence a coincidental 'preference' or 'avoidance' of the two habitat types. Future surveys could provide stronger conclusions by replicating camera surveys at the landscape scale.

Thirdly, the low and inconsistent activity of dingoes limits the conclusions that can be made about their habitat selection and role in shaping habitat use by cats. Personal observations indicate that there was not a stable population of dingoes resident at the reserve during this study. Possibly because dingoes are subject to lethal control in the region and the reserve sits just south of the 1,170 km State Barrier Fence, which was built to exclude dingoes from agricultural land in the southwest of the state, although clearly some dingoes are present 'inside' the fence.

The use of a food-based lure to attract animals to the cameras could potentially have biased the detections towards animals that are younger, less experienced hunters and hence more hungry (Short et al. 2002). If the detections were biased towards hungrier animals, we might expect that observed cat activity

would be lowest in areas with greater food availability, (e.g. the young shrublands where small mammal and reptile abundance was highest). Although I did find that cat activity was lowest at the southern cameras that were dominated by recently burnt shrublands (70% of cameras), additional evidence suggests that this is likely to be a true representation of low cat activity, rather than a bias related to prey availability and the use of lures. Remote camera monitoring indicated a decline in cat activity in the southern part of the reserve between February and May, and May and August 2013 (see Figure D.2 in Appendix D). In support of this, leg-hold trapping conducted mostly in the same area resulted in 16 animals being captured in March (trap success: 1.6 animals per 100 nights) compared to just one animal in August (0.25) (Appendix C). These results corroborate the low cat activity as recorded by remote cameras around that time.

Lastly, the surveys of prey abundance using pitfall trapping and sand pad transects only partially overlapped the camera surveys in both space and time. This is because those datasets were collected as part of separate studies, which I have since used here as complements to the camera data. In acknowledging the incomplete synchrony amongst the surveys, these data were used as broad indicators of prey activity across the study site, rather than strict predictors of predator activity. Because the factors driving carnivore spatial ecology are a combination of bottom-up (e.g. prey availability) and top-down (e.g. predation and competition) forces, future studies will benefit from using a more integrated strategy that simultaneously surveys predators, prey and competitors in different habitat types and at different times of the year.

Management implications

Despite these limitations, two important conclusions can be drawn from this work to inform predator management in the study area. Firstly, previous authors have called for positive dingo management (e.g. reintroductions or ceasing of lethal control) to be used to suppress feral cat and fox populations in Australia, citing observed negative relationships between cats/foxes and dingoes (Dickman et al. 2009; Letnic et al. 2009). While there appears to be some level of temporal segregation between cats and dingoes at the study site, positive dingo management is unlikely to be sustainable in the short- to medium-term because dingoes are subject to lethal control in the region and are wide-ranging animals, so

lethal control on neighbouring properties could potentially compromise any attempt to promote dingo populations at the study site. Such actions are unlikely to be effective unless a cross-boundary, landscape-scale approach is used. Any such actions must also consider potentially conflicting social, economic and other biodiversity conservation concerns (Fleming et al. 2012; Johnson & Ritchie 2013). Lethal control of cats, using poison baiting for example (Appendix D), may be an appropriate alternative.

Secondly, long unburnt shrublands in the study region are important habitat for threatened malleefowl (Parsons & Gosper 2011), some passerine birds (T Doherty, *unpublished data*) and small mammal and reptile species such as the Wheatbelt stone gecko *Diplodactylus granariensis* and the little long-tailed dunnart *Sminthopsis dolichura* (Chapter 4), all of which are potential prey of feral cats (Appendix A). The high cat activity in these areas may, therefore, indicate that these species experience an increased risk of cat predation compared to fauna living in recently burnt shrublands. Since cat activity was highest in very long unburnt shrublands, control devices, such as poison baits, could be concentrated in these areas to maximise their encounter rate by cats. Similarly, control activities could be focussed on areas with high rabbit abundance and in the northern part of the reserve where cat activity was highest. In any case, active monitoring and evaluation of outcomes is essential for developing effective and efficient predator control programmes.

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Chapter 4.

Response of a shrubland mammal and reptile community to a history of landscape-scale wildfire

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Preface

As published, this chapter assesses how the fire history of shrublands influences a small mammal and reptile community and discusses potential threats from altered fire regimes. The implications of the observed patterns regarding feral cat predation are discussed in Chapter 6. Eleven of the 15 study species have previously been recorded in the diet of feral cats, as have similar-sized congeners for the remaining four species (Appendix A).

Introduction

Wildfire plays an important role in structuring plant and animal communities in fire-prone regions (Whelan et al. 2002). Many species tend to show a strong response to fire and a large number of studies can be found that show either positive (Ashton et al. 2008; Conway et al. 2010; Rogers et al. 2013; Venne & Frederick 2013), negative (Baker et al. 2010; Horn et al. 2012) or mixed effects (Briani et al. 2004; Ukmar et al. 2007; Valentine et al. 2012; Albanesi et al. 2014) of fire on the occurrence, abundance and richness of a suite of vertebrate taxa. The diversity of responses is a product of the life history, dispersal capacity and autecology of the species involved, as well as the effects of fire on habitat through changes in food and shelter availability (Whelan et al. 2002). Species within broad taxonomic groups do not necessarily respond to fire in the same way, so reconciling the competing needs of different species can be difficult. Recent attempts to do so for birds in fire-prone Mediterranean landscapes have demonstrated the need to consider species autecology and habitat preferences in

conservation planning (Vallecillo et al. 2013). The state of knowledge, however, remains poor for many taxa, especially reptiles and small mammals, and for many habitats, including non-forest habitats such as shrublands.

The immediate effect of fire on fauna includes animal mortality and in the weeks following a fire, surviving animals may increase their movement in search of new shelter or disperse to more suitable habitat (Legge et al. 2008; Driscoll et al. 2012). As vegetation recovers over the longer term, changes in the availability of key resources like food (Vernes et al. 2004), nesting sites (Kern et al. 2012) and woody debris (Haney et al. 2008) alter fauna habitat suitability and hence cause successional changes in fauna communities. For example, vegetation cover, which generally increases with time since fire, influences thermoregulatory opportunities for reptiles, so distinct species assemblages are often suited to either early or late post-fire habitats (Daly et al. 2008; Santos & Cheylan 2013). Vegetation cover also provides protection from predators (Sutherland & Dickman 1999) and post-fire successional stages that have higher cover can reduce predation pressure for prey species (Torre & Díaz 2004; Conner et al. 2011).

Fire can also threaten human lives and property, so land managers frequently use prescribed burning to reduce the risk of uncontrollable fires (Fernandes & Botelho 2003). Such practices may not always be consistent with nature conservation objectives (Morrison et al. 1996; Parr & Andersen 2006) and inappropriate fire regimes, including fire return intervals, threaten many plant and animal species (Trinder-Smith et al. 1996; Buist et al. 2002; Pardon et al. 2003; Ager et al. 2007; Baker et al. 2010). Both uncontrolled wildfires and fire management that homogenises large areas of habitat through either fire exclusion or frequent burning may threaten species that specialise in distinct post-fire stages (Driscoll & Henderson 2008). An understanding of fauna responses to fire is essential to fire management that protects ecological values and built assets (Driscoll et al. 2010).

In this study, we investigated how small mammals and reptiles respond to habitat structure and fire history in semi-arid south-western Australia, an area where native fauna species are threatened by inappropriate fire regimes, introduced herbivores and predators, and interactions between these factors

(National Land and Water Resources Audit, 2001). The uncleared vegetation in our study area supports fauna species that have been extirpated or confined to small remnants in the heavily fragmented adjoining Wheatbelt region (Smith et al. 1997). However, this area is also subject to larger and more frequent fires than nearby fragmented patches of vegetation (Parsons & Gosper 2011) and several landscape-scale fires burnt large areas of vegetation (i.e. > 20,000 ha) in the study area between 2000 and 2002 inclusive. How the fire history of vegetation influences fauna communities and their habitat in this region is not well understood. Using a 4-year dataset we examined (1) how fauna habitat changes between different vegetation fire histories (recently burnt: 8–13 years since last fire; long unburnt: 25–50 years); (2) how fauna abundance is influenced by fire history; and (3) the relationship between fauna abundance and microhabitat variables. We discuss the management implications of these relationships for managing wildfire across the landscape.

Methods

Study area

We conducted this study at Charles Darwin Reserve (CDR), a 68,000-ha pastoral lease 350 km north-east of Perth (29°35'S, 116°58'E; Figure 4.1), managed for conservation by Bush Heritage Australia and de-stocked of sheep and goats since 2003. The climate is semi-arid Mediterranean, with cool winters, hot summers and unreliable, low rainfall (mean 306 mm year⁻¹ at the adjacent Wanarra pastoral station; Bureau of Meteorology 2014). Dense mixed-species shrublands on deep yellow sands (where most of the fires occur) comprise 50% of the reserve's area and the remainder is a mixture of eucalypt woodlands and other vegetation types (Braun 2006). The shrublands are dominated by *Acacia* species, but also contain other shrub genera like *Allocasuarina*, *Melaleuca*, *Hakea* and *Grevillea*. A history of unplanned fire at CDR has resulted in around 69% of these shrublands being burnt in wildfires between ~1969 and 2004 (Braun 2006). The most recent fires were between 2000 and 2004, and the oldest mapped fire scar is dated 1969, and is a collection of fire scars visible on the earliest aerial photographs available for the study site (1969) representing several fires of similar age from around that time (Braun 2006). Any areas of vegetation on the 1969 aerial photographs that did not look to have been recently burnt around that

time were classified as ‘very long unburnt’, although we did not sample in these areas. Fires in the study region predominantly occur in the sandplain shrublands, with the woodlands remaining largely unburnt, except at the edges, because the woodlands lack the dense flammable understorey found in the shrublands.

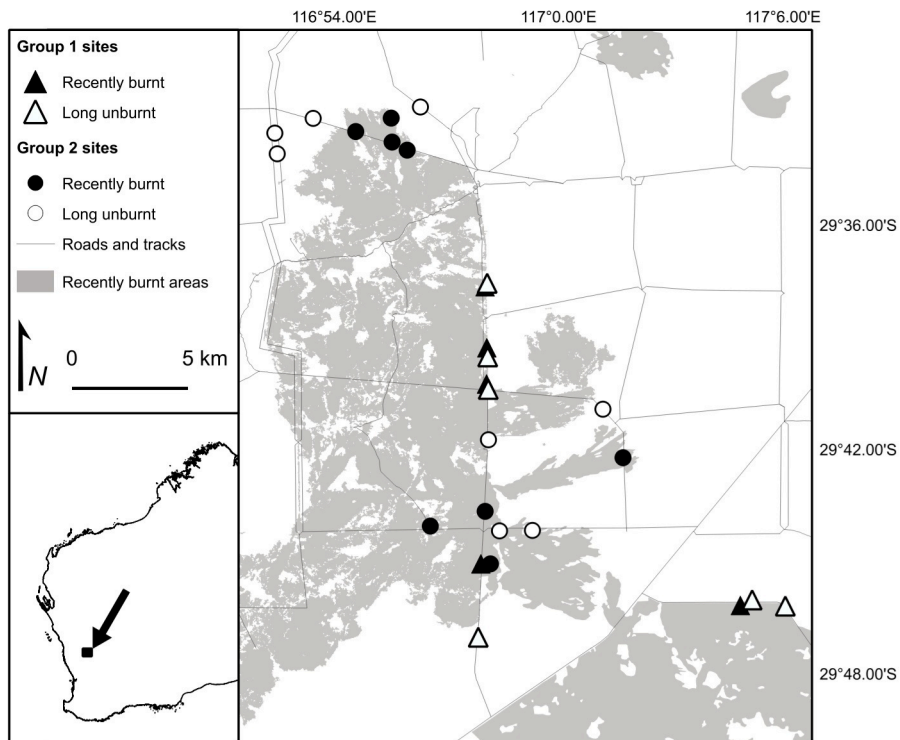


Figure 4.1 Location of recently burnt sites (black symbols) and long unburnt sites (white symbols) in the study area. Group 1 sites are triangles and Group 2 sites are circles. Grey shaded areas were aged 8–13 years since last fire at time of sampling (‘recently burnt’) and the remaining area was mostly long unburnt (25–50 years) or very long unburnt (> 50 years).

Survey design and data collection

Small mammals and reptiles were surveyed using pitfall trapping at 27 shrubland sites in the austral spring (October–November) and autumn (April–May) between 2010 and 2013 (Table 4.1). We used pitfall trapping because this technique is commonly used to compare fauna communities between areas with varying habitat structure, and previous studies have found that habitat structure does not influence animal pitfall capture probabilities (Schlesinger 2007; Craig et al. 2009; Smith et al. 2012a). Traps were open for between seven and 19 nights during each period. Two fire histories of shrubland were sampled: mid-seral sites that were burnt 8–13 years before sampling (‘recently burnt’, $n = 13$), and long

unburnt sites that were last burnt 25–50 years previously ('long unburnt', $n = 14$; Table 4.1, Figure 4.1). Two 25–26-year-old sites were included in the long unburnt group because previous studies from this system indicate that the structure of vegetation at such sites is more similar to older vegetation (~40 years old) than to younger vegetation (~10 years old) (Parsons & Gosper 2011). Recent fire frequency was reasonably consistent between sites because all of the 8–13-year-old sites were last burnt around 1969, with no fires in between, although one site was burnt in 1985 and then again in 2002, but not in 1969.

Sites were sampled across two time spans: Group 1 sites were sampled in the first three trapping periods, whereas Group 2 sites were sampled in the latter three (Table 4.1). The trapping array at Group 1 sites consisted of two parallel 25-cm-high aluminium drift fences 60 m in length and separated by ~30 m. Six pitfall traps (20-L buckets) were situated at 10-m intervals along each fence, with the fence running over the top of each trap and 5 m of fence extending out from the two end traps. Three funnel traps were randomly positioned along each fence. The same array was used at Group 2 sites, except two of the traps on each line were 60-cm-deep PVC pipes instead of buckets and no funnel traps were used. Shelter was provided in the bottom of traps to provide captured animals with protection from weather and predation. Traps were checked early each morning and any captured animals were identified to species, temporarily marked with a non-toxic paint pen and then released at the site of capture. Reptile and mammal taxonomy follow Doughty (2014) and Van Dyck and Strahan (2008) respectively. Trapping methods were approved by the Edith Cowan University Animal Ethics Committee (permits 5630 and 8501) and field research permits were issued by the Western Australian Department of Parks and Wildlife (formerly DEC) (permits SF008255 and SF008871).

Table 4.1 Summary of trapping sites indicating number of years since last fire at time of sampling and number of nights that traps were open during each trapping period.

Group 1	Site	Fire age (years)	Spring 2010 (October–November)	Autumn 2011 (April–May)	Spring 2011 (October)	
Recently burnt	A10	10–11	7	8	11	
	C10	10–11	19	8	11	
	E10	10–11	19	8	11	
	G10	10–11	7	8	11	
	J10	8–9	19	8	11	
	Long unburnt	B10	~41–50	7	8	11
		D10	~41–50	19	8	11
		F10	~41–50	19	8	11
		H10	33–34	7	8	11
		K10	25–26	19	8	11
M10	25–26	19	8	11		
Group 2	Site	Fire age (years)	Spring 2012 (October)	Autumn 2013 (April)	Spring 2013 (October)	
Recently burnt	A12	12–13	10	8	10	
	B12	12–13	10	8	10	
	C12	12–13	10	8	10	
	D12	12–13	10	8	10	
	Q12	12–13	10	8	10	
	R12	10–11	10	8	10	
	S12	12–13	10	8	10	
	T12	10–11	10	8	10	
Long unburnt	J12	~43–50	10	8	10	
	K12	~43–50	10	8	10	
	L12	~43–50	10	8	10	
	M12	~43–50	10	8	10	
	W12	~43–50	10	8	10	
	X12	~43–50	10	8	10	
	Y12	~43–50	10	8	10	
	Z12	~43–50	10	8	10	

To examine the influence of fire history on habitat structure, we measured vegetation characteristics at each of the trapping sites using two 30-m transects in June and July 2013. Each transect ran perpendicular to a drift fence, with one intersecting at the 20-m mark on one fence and the other at 40 m on the second fence. At 1-m intervals we counted the number of touches of live and dead vegetation on a 2-m pole in the following strata: 0–25, 25–50, 50–100 and 100–200 cm. At 2-m intervals we made visual estimates of the percentage bare ground and cover of litter (leaves, twigs, debris) in a 50 50-cm quadrat. We measured canopy cover using a spherical crown densiometer from a height of 1 m and counted the number of pieces of woody debris (diameter > 10 mm) that intersected transects. We measured the size of shrub patches by recording the

start and end points where patches intersected transects. Patches were defined as areas of live and dead standing vegetation in the 0–100-cm stratum, > 20 cm in length along the transect. We considered two patches independent if the distance between them was > 20 cm.

Statistical analyses

We performed permutational multivariate analysis of variance (PERMANOVA) on the habitat variables to identify whether overall structure was significantly different between recently burnt and long unburnt sites. A Euclidean resemblance matrix was created using normalised variables before running the analysis with 9,999 permutations. We performed *t*-tests to examine the influence of fire history (recently burnt or long unburnt) on mean vegetation and microhabitat variables for each site. We performed logit-transformation on variables measured as a percentage (bare ground, litter cover, canopy cover) (Warton & Hui 2011). Normality and heteroscedasticity of habitat variables were checked using Q-Q plots, box plots and residual plots. To meet the assumptions of ANOVA, we log-transformed pole count data, patch size and counts of woody debris (Zar 2010).

Only 15 species that were caught in at least 20% of the possible 81 site-session combinations were analysed. We used linear mixed models to test the effect of fire history on fauna abundance. We included the number of trap-nights in each survey period as an offset to account for varying sampling effort. Fire history was included in the model as a fixed effect with two levels: recently burnt and long unburnt. Both burnt and unburnt sites were surveyed in each group (1 or 2) and every survey period (season-year), so we fitted group and period as random intercepts, which accounts for additional variation and enables us to test fire response across all sites. We fitted site as a random intercept to account for repeat sampling of the same sites over time. We fitted both Poisson and negative binomial models for each species and inspected the residual plots to determine which distribution best fit the data (further details can be found in Figure 4.4 in Supplementary material p76). We then calculated 90% profile confidence intervals for the effect of fire history on the fixed effect parameter estimates using the chosen error distribution. We followed previous authors (Driscoll & Henderson 2008; Smith et al. 2013) and set the significance level at $\alpha = 0.1$, which minimises

the Type II error rate, a favourable approach when the potentially harmful consequences of a Type II error are high (Field et al. 2004). Given the complications associated with significance testing in a mixed modelling framework (Pinheiro & Bates 2000), we inferred 'significant' differences in abundance where the confidence intervals did not overlap zero. The reference level in the fixed effect was 'recently burnt'. The residual errors of each model were inspected visually for normality to ensure model validity. For graphical illustration, we standardised capture data (number of captures per 100 nights) to account for varying sampling effort across trapping periods.

We investigated the influence of microhabitat variables on fauna abundance using Poisson linear mixed models after removing highly correlated predictor variables, namely number of vegetation touches at 25–50 cm ($r_{25} = 0.70$ with 0–25 cm), litter cover ($r_{25} > \pm 0.78$ with 100–200 cm, bare ground and canopy cover) and canopy cover ($r_{25} > \pm 0.73$ with 100–200 cm, bare ground and litter cover). We pooled capture data for each site across all trapping sessions because microhabitat variables were measured once only and are unlikely to have changed much during the study period. We included the number of trap–nights in each survey period as an offset to account for varying sampling effort and set group as a random intercept. We fitted single-term models for each untransformed microhabitat variable (0–25, 50–100, 100–200 cm, bare ground, patch size and number of pieces of woody debris) and ranked them against a null model using the second-order Akaike Information Criterion (AIC_c). For any well supported models ($\Delta AIC_c < 2$ and a weight > 0.2), we calculated 95% confidence intervals to test the effect of the microhabitat variable on species abundance. We present plots of any significant relationships. All analyses were done in programme R version 2.14.2 using the lme4 package version 1.0–5 and the vegan package version 2.0–9 (R Development Core Team 2012; Oksanen et al. 2013; Bates et al. 2014).

Results

Fire and habitat structure

Vegetation structure differed significantly in PERMANOVA between recently burnt and long unburnt habitat (pseudo- $F_{1,25} = 24.21$, $P < 0.001$). There was no difference in vegetation structure between recently burnt and long unburnt sites in the 0-25 cm ($t_{24.58} = 1.12$, $P = 0.275$), 25-50 cm ($t_{21.57} = 0.62$, $P = 0.539$) and 50-100 cm strata ($t_{24.89} = 1.67$, $P = 0.107$). The number of vegetation touches in the 100-200 cm layer at long unburnt sites was almost three times greater than at recently burnt sites ($t_{20.96} = -5.07$, $P < 0.001$), percentage litter cover at long unburnt sites was more than twice that at recently burnt sites ($t_{25.99} = -6.31$, $P < 0.001$) and canopy cover was more than 10 times greater at long unburnt sites ($t_{19.67} = -8.22$, $P < 0.001$), whereas percentage bare ground was 40% lower at long unburnt sites ($t_{25.98} = 5.76$, $P < 0.001$). Patch size ($t_{18.18} = -1.66$, $P = 0.113$) and woody debris ($t_{25.96} = -1.41$, $P = 0.170$) did not differ between recently burnt and long unburnt sites.

Fauna response to fire history

Across the six sampling periods, traps were open for a total of 12,036 trap-nights and we captured 1,455 reptiles from 34 species and 294 mammals from seven species (Dragons: 5 species; Elapid snakes: 5; Geckoes: 8; Legless lizards: 3; Skinks: 10; Blind snakes: 1; Monitors: 2; Dasyurid marsupials: 4; Rodents: 3; see Table 4.4 in *Supplementary material*). The most commonly captured reptiles were the skinks *Ctenotus schomburgkii* ($n = 545$) and *Liopholis inornata* ($n = 116$) and the geckoes *Diplodactylus pulcher* ($n = 276$) and *D. granariensis* ($n = 110$). The most commonly caught mammals were the native mouse *Pseudomys hermannsburgensis* ($n = 83$) and the dasyurids *Sminthopsis crassicaudata* ($n = 66$) and *S. dolichura* ($n = 68$).

Five of the 15 species were most abundant in recently burnt habitat (two dasyurid marsupials and three lizards) and four species were most abundant in long unburnt habitat (one dasyurid and three lizards; Table 4.2, Figure 4.2). The abundance of the remaining six species was similar between the two fire histories (two rodents and four lizards; Table 4.2, Figure 4.2).

Table 4.2 Parameter estimates and 90% confidence intervals from the fitted models for the effect of vegetation fire history on species abundance. ‘Recently burnt’ was used as the reference level in the fixed effect. ‘Significant’ fire effects were inferred where the confidence intervals of the ‘long unburnt’ estimate did not overlap zero. Significant relationships are indicated with a *.

Species	Model ^A	Intercept estimate	90% CI	Long unburnt estimate	90% CI	Observed response ^B
<i>Ctenophorus maculatus</i> *	NB	-2.69	-3.29, -2.09	-1.46	-2.31, -0.61	B
<i>Ctenophorus scutulatus</i> *	NB	-4.68	-6.49, -2.86	1.16	0.27, 2.04	UB
<i>Diplodactylus granariensis</i> *	P	-2.54	-3.45, -1.70	0.50	0.15, 0.84	UB
<i>Diplodactylus pulcher</i>	NB	-1.75	-2.43, -1.07	0.13	-0.41, 0.68	-
<i>Lucasium maini</i> *	NB	-2.85	-3.78, -1.92	-2.30	-3.20, -1.40	B
<i>Ctenotus mimetes</i> *	NB	-4.28	-5.55, -3.00	0.89	0.10, 1.67	UB
<i>Ctenotus pantherinus</i>	P	-5.36	-8.87, -3.76	-0.66	-3.31, 1.55	-
<i>Ctenotus schomburgkii</i>	P	-0.42	-1.39, 0.55	-0.29	-0.64, 0.04	-
<i>Liopholis inornata</i> *	P	-1.96	-2.76, -1.33	-1.34	-2.23, -0.56	B
<i>Menetia greyii</i>	NB	-4.92	-6.57, -3.27	0.63	-0.25, 1.51	-
<i>Sminthopsis crassicaudata</i> *	P	-2.37	-3.63, -1.21	-1.33	-1.86, -0.80	B
<i>Sminthopsis dolichura</i> *	P	-3.02	-3.43, -2.67	0.85	0.42, 1.32	UB
<i>Sminthopsis gilberti</i> *	P	-3.56	-4.56, -2.75	-0.82	-1.69, -0.03	B
<i>Notomys mitchellii</i>	P	-4.30	-6.24, -2.36	-0.48	-1.15, 0.20	-
<i>Pseudomys hermannsburgensis</i>	P	-2.43	-3.31, -1.63	-0.27	-0.69, 0.16	-

^A Model error distribution: NB, negative binomial; P, Poisson.

^B B, recently burnt; UB, long unburnt; dash, nil response.

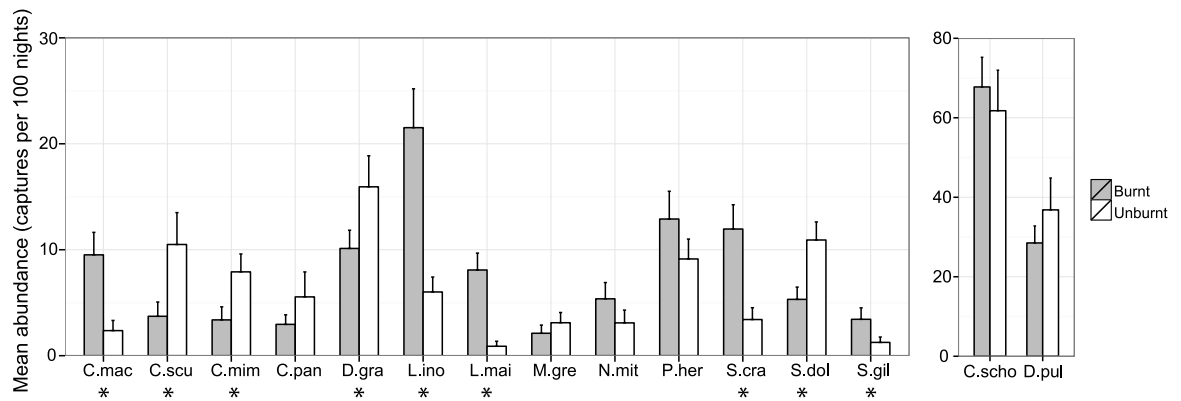


Figure 4.2 Mean abundance per 100 nights and standard error bars for recently burnt and long unburnt habitat. *statistically significant difference. C.mac, *Ctenophorus maculatus*; C.scu, *Ctenophorus scutulatus*; C.mim, *Ctenotus mimetes*; C.pan, *Ctenotus pantherinus*; D.gra, *Diplodactylus granariensis*; L.ino, *Liopholis inornata*; L.mai, *Lucasium maini*; M.gre, *Menetia greyii*; N.mit, *Notomys mitchellii*; P.her, *Pseudomys hermannsburgensis*; S.cra, *Sminthopsis crassicaudata*; S.dol, *Sminthopsis dolichura*; S.gil, *Sminthopsis gilberti*; C.scho, *Ctenotus schomburgkii*; D.pul, *Diplodactylus pulcher*.

Fauna response to microhabitat structure

Fourteen microhabitats models were well supported (Table 4.5 in *Supplementary material*) and 11 of these relationships were significant (Table 4.3). *Ctenophorus maculatus* abundance increased with greater amounts of bare ground and less vegetation touches in the 50–100-cm stratum (Figure 4.3a–b). *Ctenophorus scutulatus* abundance decreased with the number of touches in the 0–25-cm stratum, although the relationship was weak (Figure 4.3c). *Diplodactylus pulcher* abundance increased with greater amounts of bare ground and *Lucasium maini* abundance was negatively correlated with the number of touches in the 100–200-cm stratum (Figure 4.3d–e). *Ctenotus mimetes* abundance increased with greater patch size and *C. schomburgkii* abundance increased with greater amounts of woody debris, although the confidence bands for the latter were wide (Figure 4.3f–g). *Ctenotus pantherinus* abundance showed a very weak positive relationship with the number of touches in the 0–25-cm stratum (Figure 4.3h). *Liopholis inornata* abundance had a weak negative relationship with the number of touches in the 100–200-cm stratum (Figure 4.3i). *Sminthopsis crassicaudata* abundance increased with greater amounts of bare ground and *P. hermannsburgensis* abundance increased with greater amounts of woody debris (Figure 4.3j–k).

Table 4.3 Parameter estimates and 95% confidence intervals for microhabitat models that were well supported. Significant relationships are indicated with a *. Complete modelling results are given in Table 4.5 in Supplementary material p78

Species	Microhabitat variable	Model estimate	95% CI
<i>Ctenophorus maculatus</i>	Touches at 50–100 cm	-1.50*	-2.53, -0.50
<i>Ctenophorus maculatus</i>	% bare ground	0.03*	0.01, 0.05
<i>Ctenophorus scutulatus</i>	Touches at 0–25 cm	-0.93*	-1.60, -0.42
<i>Diplodactylus pulcher</i>	% bare ground	0.016*	0.009, 0.024
<i>Lucasium maini</i>	Touches at 100–200 cm	-0.62*	-1.16, -0.12
<i>Ctenotus mimetes</i>	Patch size	0.81*	0.42, 1.17
<i>Ctenotus pantherinus</i>	Touches at 0–25 cm	0.42*	0.12, 0.69
<i>Ctenotus schomburgkii</i>	Number of pieces of woody debris	0.013*	0.007, 0.020
<i>Liopholis inornata</i>	Touches at 100–200 cm	-0.45*	-0.75, -0.15
<i>Menetia greyii</i>	Touches at 50–100 cm	1.25	-0.10, 2.66
<i>Sminthopsis crassicaudata</i>	% bare ground	0.04*	0.02, 0.06
<i>Sminthopsis dolichura</i>	Touches at 50–100 cm	0.70	-0.06, 1.48
<i>Sminthopsis gilberti</i>	Touches at 50–100 cm	-1.59	-3.09, 0.01
<i>Pseudomys hermannsburgensis</i>	Number of pieces of woody debris	0.03*	0.01, 0.05

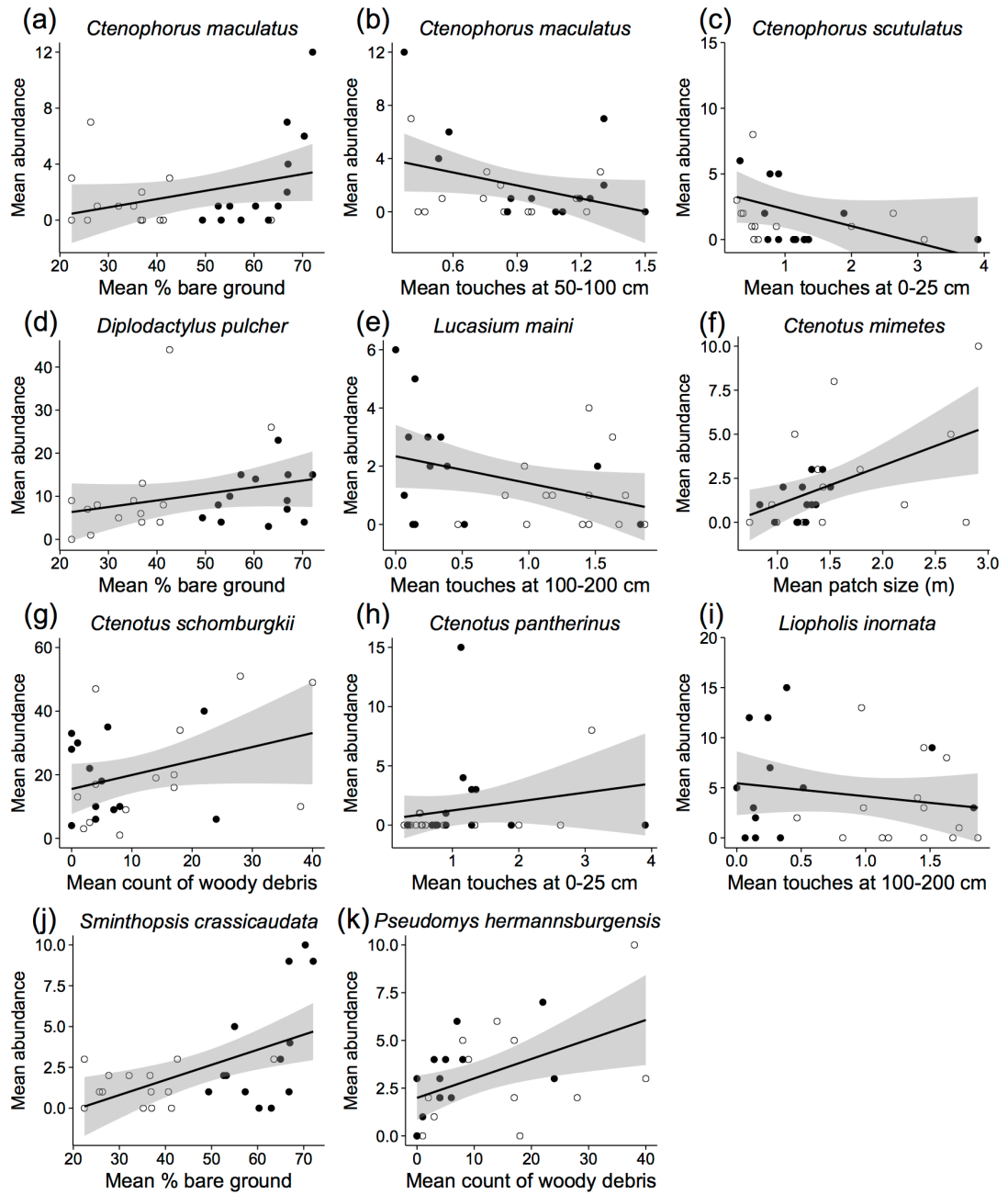


Figure 4.3 Significant mixed modelling relationships between species abundance and microhabitat variables. Recently burnt sites are solid black circles and long unburnt sites are white circles with a black outline. The solid black line is the fitted model and the shaded area is the 95% confidence band.

Discussion

Our study has revealed that the shrubland mammal and reptile species studied here show divergent responses to fire-induced habitat changes. The two fire ages that we sampled were structurally distinct from each other: long unburnt sites had taller and denser vegetation, whereas more recently burnt sites lacked a distinct canopy, were dominated by lower strata and had larger areas of bare ground. Although the younger vegetation is 8–13 years since last fire, these areas are still in a post-fire recovery stage and vegetation attributes are expected to develop further as time since fire increases. Shrubland fire history has a strong influence on vegetation structure and in turn influences habitat suitability for fauna species.

Fauna response to fire history

Nine of our 15 study species showed a significant response to fire history: five were most abundant in recently burnt habitat and four were most abundant in long unburnt habitat. Our finding that the commonly captured skink *Liopholis inornata* was most abundant in younger shrubland fire ages is supported by similar findings in mallee woodland and desert ecosystems (Caughley 1985; Pianka & Goodyear 2011; Nimmo et al. 2012a). For the remaining species, fire response information across a range of vegetation types is lacking and requires further studies for general patterns to be drawn out. A caveat of our findings is that the number of species displaying differential habitat use may have been greater if an immediate post-fire age (0–3 years) was sampled, although no such area was available at the time of this study.

We found that fire responses were variable within taxonomic groups; for example the dragon *Ctenophorus maculatus* was most abundant at recently burnt sites, whereas *C. scutulatus* was more abundant at long unburnt sites. Similarly, two of the marsupial dunnarts (*Sminthopsis crassicaudata* and *S. gilberti*) were most abundant in recently burnt habitat, but a third was most abundant in long unburnt areas (*S. dolichura*). Differing responses to fire history across species have been recorded in other Mediterranean-type shrublands (Herrando et al. 2002; Rochester et al. 2010; Santos & Cheylan 2013) and may be indicative of local habitat partitioning whereby each species is adapted to exploiting the resources of

a distinct post-fire habitat (Daly et al. 2008). Faunal response to fire can be influenced by multiple biotic and abiotic factors including taxonomy (Santos & Cheylan 2013), life history (Caughley 1985), resource availability (Pastro et al. 2013) and predation pressure (Conner et al. 2011), and a single species' response can vary across spatial gradients (Nimmo et al. 2012a; Nimmo et al. 2014). Identifying the exact mechanisms responsible for the patterns reported here requires manipulative experiments or observations of foraging behaviour and movement patterns.

One of the species that did not show any response to fire history in our study (*Ctenotus schomburgkii*) was actually found to be most abundant in long unburnt mallee woodlands in southern Australia when compared with more recently burnt mallee (Smith et al. 2013). The contrasting findings between that study and ours are not due to the fire histories sampled because *C. schomburgkii* was common in both our 8–13 and 25–50-year-old vegetation, whereas Smith et al. (2013) detected low capture rates between 5 and 20 years and much higher capture rates in areas > 40 years old. *Ctenotus schomburgkii* has a very wide distribution, so it is conceivable that its response to fire history may vary between the different vegetation types. Regional differences in a species response to fire history have important implications for land managers (Nimmo et al. 2012a; Nimmo et al. 2014). An unnecessary management intervention would occur if the findings from the previous study were used to justify fire suppression to promote *C. schomburgkii* habitat in the current study area. When establishing fire management plans that promote biodiversity values, we recommend that land managers exercise caution in adopting species-specific information from different locations and broad vegetation types, although we understand that this is challenging given the lack of information available for many ecosystems.

Fauna response to microhabitat structure

Site-based differences in microhabitat availability can also help explain patterns in fauna species abundance. In our study, the abundance of 10 species was related to microhabitat variables like woody debris, patch size and bare ground, although the trends for *Ctenophorus scutulatus*, *Diplodactylus pulcher*, *Ctenotus schomburgkii*, *C. pantherinus* and *Liopholis inornata* were weak (Figure 4.3c–d, g–i) and are not discussed further here.

The positive relationship between *Sminthopsis crassicaudata* abundance and bare ground is logical because this species has been recorded elsewhere using saltpan and short shrubland habitats (Read 1987; McKenzie et al. 2003) and bare ground was greatest in our younger fire ages. Also, the relationship between *Ctenophorus maculatus* abundance, bare ground and vegetation structure at 50–100 cm is probably related to this species' higher abundance in recently burnt habitat. Larger areas of bare ground and shorter vegetation may afford this species better thermoregulatory opportunities, although little is known about its behaviour. Similarly, the positive relationship between *Lucasium maini* abundance and vegetation structure in the upper stratum is probably related to this species' higher abundance in recently burnt habitat.

The positive relationship between *P. hermannsburgensis* abundance and woody debris is interesting because this species is a small rodent not known to be reliant on woody debris. This species' abundance did not vary according to fire history, nor did amounts of woody debris, so woody debris may be acting as a surrogate for an unmeasured variable influencing *P. hermannsburgensis* abundance, such as food or shelter availability. In an experimental manipulation of fire in arid grasslands, Southgate and Masters (1996) also found no difference in the abundance of *P. hermannsburgensis* between burnt and unburnt plots, so it is likely that this species is relatively tolerant of fire-induced changes in habitat.

The skink *Ctenotus mimetes* was most abundant in long unburnt vegetation, but its positive response to vegetation patch size across was evident across both fire histories. Greater patch size may be related to increased food availability or greater refuge from predators, although detailed studies are needed to identify the exact causal mechanism.

Synthesis and applications

The threats to small mammals and reptiles are a complex interaction between multiple biotic and abiotic drivers that need to be managed concurrently. Species with specialist habitat requirements are more at risk from inappropriate fire regimes than are species that are able to exploit a range of post-fire ages (Driscoll & Henderson 2008). Just over half of our study species were most abundant in either the recently burnt or long unburnt areas, so careful

management of fire may be needed to maximise habitat suitability across the landscape. Removal of long unburnt vegetation by fire across large areas may threaten late successional species by creating sub-optimal habitat, and creation of open areas by fire may increase predation pressure by creating better hunting opportunities for predators (Conner et al. 2011; McGregor et al. 2014). Additionally, large uncontrolled fires are particularly threatening because while it is easy to create recently burnt habitat, long unburnt habitat takes decades to recover (Parsons & Gosper 2011). Across the study landscape only around 25% of the shrublands remain long unburnt (Braun 2006). Unburnt patches of vegetation can provide refuges that allow fauna to persist in post-fire landscapes (Robinson et al. 2013) and given that some species are most abundant in the long unburnt fire ages, we recommend that fire management should aim to preserve areas of long unburnt vegetation (> 40 years post-fire).

On the contrary, complete fire suppression is likely to threaten species that are most abundant in earlier post-fire ages. Around 30% of the study site is currently ~13 years since last fire (Braun 2006), so mid-seral species are likely to be adequately catered for at present. However, the availability of these younger fire ages will decline as the vegetation ages without any new fires. It is therefore important to plan over the longer term for all species requirements. Although most fires in the study region are unplanned wildfires, targeted prescribed burning may be needed in the future if there are no unplanned fires over the next 15–30 years. Systematic mapping of regional fire histories complemented by information on animal ecology is essential to the strategies that we have described above, as well as broader fire management strategies that aim to promote animal diversity at the landscape scale (Driscoll et al. 2010; Avitabile et al. 2013). Such strategies should also consider the potentially competing habitat requirements of other taxa within this system, such as bird and plant communities. We recommend that information on animal responses to fire is best gained through approaches that adopt principles of adaptive management and experimental design. Future prescribed burns or unplanned fires will present valuable opportunities to examine the immediate post-fire responses of mammal and reptile species. Additionally, future research should investigate the post-fire response of other taxonomic groups, like

avifauna, about which very little is known in Australian shrublands (Woinarski & Recher 1997).

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Supplementary material

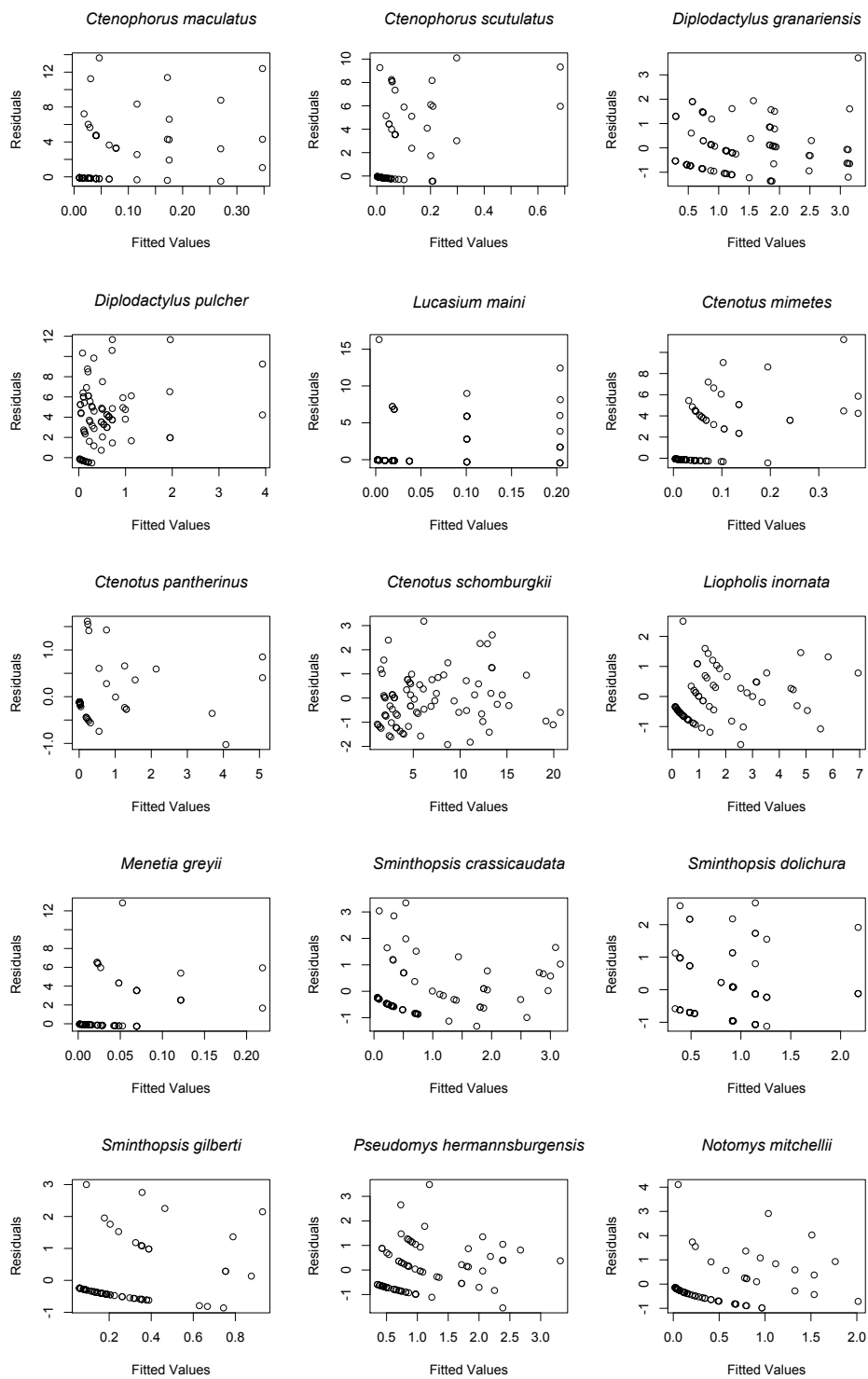


Figure 4.4 Plots of residual and fitted values for linear mixed models to test the effect of vegetation fire age on fauna species abundance. The error distribution used in each model is listed in Table 4.2 in the main document.

Table 4.4 List of reptile and mammal species captured during monitoring at Charles Darwin Reserve, Western Australia in 2010–2013.

Skinks	Dragons
<i>Ctenotus mimetes</i>	<i>Ctenophorus maculatus</i>
<i>Ctenotus pantherinus</i>	<i>Ctenophorus reticulatus</i>
<i>Ctenotus schomburgkii</i>	<i>Ctenophorus scutulatus</i>
<i>Ctenotus severus</i>	<i>Moloch horridus</i>
<i>Egernia depressa</i>	<i>Pogona minor</i>
<i>Liopholis inornata</i>	Snakes
<i>Lerista muelleri</i>	<i>Brachyuropsis semifasciata</i>
<i>Menetia greyii</i>	<i>Neelaps bimaculatus</i>
<i>Morethia obscura</i>	<i>Parasuta monachus</i>
<i>Tiliqua occipitalis</i>	<i>Pseudonaja modesta</i>
	<i>Pseudonaja nuchalis</i>
Geckoes	<i>Ramphotyphlops hamatus</i>
<i>Diplodactylus granariensis</i>	Monitors
<i>Diplodactylus pulcher</i>	<i>Varanus gouldii</i>
<i>Lucasium maini</i>	<i>Varanus panoptes</i>
<i>Gehyra variegata</i>	Rodents
<i>Heteronotia binoei</i>	<i>Mus musculus</i>
<i>Rhyncodeura ornata</i>	<i>Notomys mitchellii</i>
<i>Strophurus michaelsoni</i>	<i>Pseudomys hermannsburgensis</i>
<i>Strophurus strophurus</i>	Dasyurid marsupials
Legless lizards	<i>Sminthopsis crassicaudata</i>
<i>Delma butleri</i>	<i>Sminthopsis dolichura</i>
<i>Lialis burtonis</i>	<i>Sminthopsis gilberti</i>
<i>Pygopus nigriceps</i>	<i>Sminthopsis granulipes</i>

Table 4.5 Mixed model rankings (ΔAIC_c) and weights for relationships between fauna species abundance and microhabitat variables. Models with a $\Delta AIC_c < 2$ and a weight > 0.2 were explored further and are indicated here with bold text and grey shading.

Fauna species	Null model	Touches at 0-25 cm	Touches at 50-100 cm	Touches at 100-200 cm	% bare ground	Patch size	Number of pieces of woody debris
<i>Ctenophorus maculatus</i>	ΔAIC_c : 7.82	9.17	1.58	1.87	0.00	2.35	10.07
	Weight: 0.009	0.005	0.207	0.179	0.456	0.141	0.003
<i>Ctenophorus scutulatus</i>	ΔAIC_c : 13.85	0.00	4.02	6.35	15.20	15.95	4.76
	Weight: 0.001	0.787	0.106	0.033	0.000	0.000	0.073
<i>Diplodactylus granariensis</i>	ΔAIC_c : 0.00	2.54	1.64	2.37	1.26	2.48	2.54
	Weight: 0.319	0.090	0.141	0.098	0.170	0.093	0.090
<i>Diplodactylus pulcher</i>	ΔAIC_c : 15.13	11.48	9.56	14.30	0.00	13.17	7.65
	Weight: 0.001	0.003	0.008	0.001	0.965	0.001	0.021
<i>Lucasium maini</i>	ΔAIC_c : 3.34	5.79	5.21	0.00	4.31	3.01	3.55
	Weight: 0.103	0.030	0.040	0.548	0.064	0.122	0.093
<i>Ctenotus mimetes</i>	ΔAIC_c : 13.09	12.47	15.13	14.26	15.45	0.00	15.59
	Weight: 0.001	0.002	0.001	0.001	0.000	0.994	0.000
<i>Ctenotus pantherinus</i>	ΔAIC_c : 4.53	0.00	6.11	3.16	3.56	3.38	3.83
	Weight: 0.056	0.538	0.025	0.111	0.091	0.099	0.079
<i>Ctenotus schomburgkii</i>	ΔAIC_c : 13.28	7.98	14.55	15.83	12.46	11.29	0.00
	Weight: 0.001	0.018	0.001	0.000	0.002	0.003	0.974
<i>Liopholis inornata</i>	ΔAIC_c : 6.15	8.09	7.41	0.00	8.70	7.03	6.68
	Weight: 0.040	0.015	0.021	0.857	0.011	0.026	0.030
<i>Menetia greyii</i>	ΔAIC_c : 0.75	3.20	0.00	2.90	1.32	2.18	3.20
	Weight: 0.216	0.064	0.315	0.074	0.162	0.106	0.064
<i>Sminthopsis crassicaudata</i>	ΔAIC_c : 18.47	16.06	20.69	9.55	0.00	9.55	19.11
	Weight: 0.000	0.000	0.000	0.008	0.983	0.008	0.000
<i>Sminthopsis dolichura</i>	ΔAIC_c : 0.70	3.12	0.00	1.40	2.44	1.99	3.04
	Weight: 0.214	0.064	0.303	0.151	0.090	0.112	0.066
<i>Sminthopsis gilberti</i>	ΔAIC_c : 1.27	3.80	0.00	3.82	2.63	3.77	3.40
	Weight: 0.218	0.062	0.411	0.061	0.110	0.063	0.075
<i>Notomys mitchellii</i>	ΔAIC_c : 0.00	1.87	0.99	2.49	0.84	1.85	0.76
	Weight: 0.248	0.097	0.152	0.071	0.163	0.098	0.170
<i>Pseudomys hermannsburgensis</i>	ΔAIC_c : 8.65	8.64	6.15	11.18	11.09	7.56	0.00
	Weight: 0.012	0.012	0.042	0.003	0.004	0.021	0.907

Chapter 5.

A game of cat-and-mouse: microhabitat influences rodent foraging in recently burnt, but not long unburnt shrublands

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Introduction

Vegetation cover provides small mammals with food, shelter, nesting sites and refuge from predators (Sutherland & Dickman 1999; Monamy & Fox 2000). Small mammals assess predation risk using indirect cues and minimise predator encounters by modifying their activity (Lima & Dill 1990; Rosenzweig 1981). Habitat structure is a well-studied cue and can indicate relative predation risk if prey vulnerability depends upon vegetation structure (Verdolin 2006). Encounters with predators are more likely to occur in open areas (Kotler et al. 1988; Dickman et al. 1991; Janssen et al. 2007) and vegetation cover plays an important role in mediating the lethal and non-lethal effects of predation on small mammals (Arthur et al. 2005; Conner et al. 2011). Structurally complex habitats can reduce predation rates by providing refuges for prey (Kotler et al. 1991). For example, in high refuge areas the survival rates and population density of house mice *Mus musculus* were higher than in low refuge areas (Arthur et al. 2005) and preferential use of complex microhabitats during times of high predator activity has been demonstrated for house mice (Dickman 1992), gerbils *Gerbillus* spp. (Abramsky et al. 1996) and Australian desert rodents (Dickman et al. 2010b). In addition to changes in predator activity, temporal changes in cover availability influence predation risk and can subsequently alter the behaviour, demographics and growth rates of prey populations (Arthur et al. 2004; Spencer et al. 2005).

Small mammals are also affected by wildfire and prescribed burning because fire alters vegetation structure and reduces cover availability (Capitanio &

Carcaillet 2008; Craig et al. 2010), which can lead to changes in small mammal community composition, particularly in fire-prone regions (Friend 1978; Fontaine & Kennedy 2012; Chapter 4). Torre and Díaz (2004) found that small mammal abundance and richness decreased with time since fire in Mediterranean forests, whereas Horn et al. (2012) found that recently burnt areas had lower small mammal abundance and richness when compared to unburnt areas in the Mojave Desert, United States. Fire can also affect the dynamics and behaviour of small mammal populations, leading to reduced population size, resource availability and individual fitness, along with increased competition (Sutherland & Dickman 1999).

The influence of vegetation cover and fire on small mammals may have a synergistic influence on predation pressure (Arthur et al. 2010; Conner et al. 2011) because reduced cover caused by fire results in less shelter for prey species and allows predators increased access to structurally complex habitats and thus better hunting opportunities (Dees et al. 2001; Birtsas et al. 2012; McGregor et al. 2014). Conner et al. (2011) found that prescribed fire resulted in higher predation rates on cotton rats *Sigmodon hispidus* because it created suboptimal habitat for the rats. Although the combined effects of fire and predation on fauna are not well understood (Sutherland & Dickman 1999), the interaction between these two processes is considered to be a contributing factor to recent declines in Australia's mammal fauna (Woinarski et al. 2010; Fisher et al. 2014a). Altered fire regimes and predation by introduced predators, such as red foxes *Vulpes vulpes* and feral cats *Felis catus*, present land managers with a formidable challenge; knowledge of how fire alters the habitat and foraging behaviour of small mammals is needed if these communities are to be conserved.

In this study, we investigated how fire history and micro-habitat structure influence risk-sensitive foraging behaviour of small rodents (*Notomys mitchellii*, *Pseudomys hermannsburgensis*, and *M. musculus*) in semi-arid shrublands in southwestern Australia. These shrublands are a fire-prone environment where canopy cover and continuity increase with time since fire (Parsons & Gosper 2011; Dalglish 2012). We expected that rodents would prefer to forage in more structurally complex habitats (i.e. sheltered microhabitat and long unburnt vegetation). We used giving-up densities (Brown 1988) to indirectly measure the influence of predation risk on foraging activity. This method, commonly used in

field experiments (e.g. Hinkelman et al. 2011; Dickman et al. 2011), predicts that an optimally foraging animal ceases foraging in an area when the benefits no longer exceed the costs (Brown 1988). In an experimental setting where other factors are controlled for, a decrease in the GUD corresponds to a decrease in perceived predation risk (Brown 1988). We conducted a two-factor field experiment in long unburnt (> 40 years since last fire) and recently burnt (9–13 years) shrublands with open and sheltered microhabitats and predicted that: (1) GUDs will be higher in recently burnt compared to long unburnt vegetation because the shorter and sparser vegetation in younger areas will provide rodents with less refuge from predators; (2) GUDs will be higher in open microhabitat when compared to sheltered microhabitat because open areas will make rodents more vulnerable to predation; and (3) the effect of microhabitat on GUDs will be weaker in long unburnt vegetation when compared to recently burnt because the taller and denser vegetation in older habitat will mediate predation risk and hence microhabitat structure will be less important there.

Materials and Methods

Study site and species

We conducted this study at Charles Darwin Reserve, a ~68,000 ha pastoral lease 350 km north-east of Perth in the northern ‘wheatbelt’ region of Western Australia (29°35’S, 116°58’E), managed for conservation by Bush Heritage Australia and destocked of goats and sheep since 2003 (Figure 5.1). The climate is semi-arid Mediterranean, with cool winters, hot summers, and unreliable, low rainfall (mean 306 mm year⁻¹ at the adjacent Wanarra pastoral station; Bureau of Meteorology 2014). Mixed *Acacia* spp. shrublands make up 50% of the reserve’s area and the remainder is a mixture of eucalypt woodlands and other shrubland types (Braun 2006). A history of unplanned fire has created a series of fire ages across the landscape: the most recent fires in *Acacia* shrubland occurred between 2000 and 2004 inclusive (‘recently burnt’: 9–13 years since last fire at time of sampling), and the oldest recorded fire age is estimated at 1969 (Braun 2006). Wildfire dramatically reduces vegetation cover in *Acacia* shrublands and vegetation attributes like canopy height and density recover over successional timeframes of decades (Parsons & Gosper 2011; Dalglish et al. 2015). Fire history information was extracted from spatial data layers in ArcMap (ESRI 2012) that

were drawn from satellite imagery and aerial photography of historical fire scars around 2005 (Braun 2006). There have been no fires at the study site since that time.

Mitchell's hopping mouse *Notomys mitchellii* and the sandy inland mouse *Pseudomys hermannsburgensis* are small native rodents found in arid and semi-arid parts of Australia (van Dyck & Strahan 2008). The hopping mouse (40–60 g) is bipedal and has large back legs, whereas *P. hermannsburgensis* is smaller (9–14.5 g) and quadrupedal (van Dyck et al. 2013). They inhabit woodlands, shrublands and hummock grasslands and forage exclusively at night mostly on seeds and other plant material, but also insects to a lesser extent (van Dyck & Strahan 2008). The life history, feeding ecology and ecological role of *P. hermannsburgensis* are very similar to those of the introduced house mouse *M. musculus* (up to 30 g), which is widespread throughout most of Australia and encompasses the distributions of both *N. mitchellii* and *P. hermannsburgensis* (van Dyck & Strahan 2008). Potential predators of rodents in the study area include the feral cat and the barn owl *Tyto alba*, and also to a lesser extent the dingo *Canis dingo*, the introduced red fox, elapid snakes and other birds of prey.

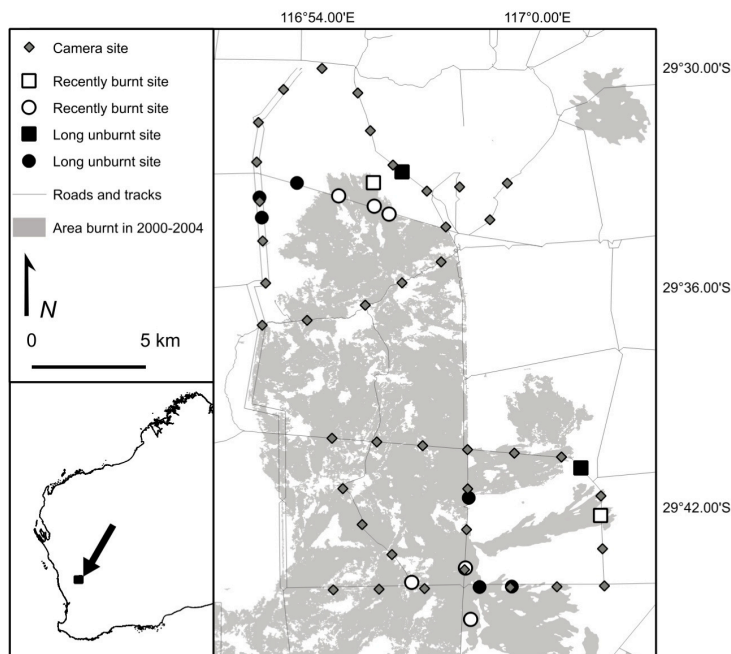


Figure 5.1 Location of recently burnt (black circles) and long unburnt (white circles) giving-up density experiment sites. Additional sites where pitfall trapping was undertaken are shown with square symbols. Small gray diamonds represent the location of remote cameras. The gray shading represents the distribution of shrublands that were last burnt 9–13 years prior to sampling, and most other areas were unburnt for > 40 years.

Foraging experiments

We established 144 feeding trays across six long unburnt and six recently burnt sites in *Acacia* shrublands in 2013. All sites were separated by a minimum distance of 1 km, except for one pair that was separated by 800 m (Figure 5.1). The long unburnt sites were situated in continuous patches of vegetation (> 40 years since last fire) ranging in size from 20 to > 200 ha and the recently burnt sites were situated in continuous areas of vegetation > 200 ha (9–13 years since last fire). At each site six trays were placed in ‘open’ microhabitat consisting of a clearing at least 3 m in diameter with no vegetation cover. Generally these clearings were naturally devoid of vegetation cover, although at some sites a small amount of dead vegetation was manually removed. The remaining six trays were placed in ‘sheltered’ microhabitat, which was positioned directly under the cover of a live shrub. All trays were separated by a minimum distance of 20 m. Feeding trays consisted of round plastic containers 5-cm deep and of 19-cm diameter. Trays were half buried in the ground and filled with 1 litre of sifted sand with 20 peanut quarters randomly mixed in. The sand in and around each tray was smoothed to detect foraging activity. Trays were checked for footprints and tracks the next morning and the remaining peanuts were counted. The GUD was recorded as the number of peanuts remaining in the tray after each night. Any missing peanuts were replaced and the sand was smoothed again. We repeated this for 6–8 nights, with the first 3–5 nights used as prebaiting to allow animals to become accustomed to feeding at trays, thus giving 3 nights of useful data for each sampling period ($n = 864$ tray-nights). We conducted 1 sampling period each in February and April 2013 \pm 5 days from the new moon phase to prevent lunar illumination from influencing foraging activity (Prugh & Golden 2014). Lids were placed on trays and trays were left in situ between sampling periods. During all experiments we identified the species responsible for foraging events based on footprints and tracks left in the sand surrounding the tray. *Notomys mitchellii* prints were identified by two long hind foot tracks > 25 mm and the imprint of the heel, while *P. hermannsburgensis* and *M. musculus* tracks were identified by their small size (< 20 mm) and imprint of five hind toes (Triggs 2004). It was not possible to distinguish between *P. hermannsburgensis* and *M. musculus* based on footprints and tracks, so we refer to them collectively as “mouse group” in the results.

Rodent abundance

We conducted pitfall trapping at the study site in the austral spring 2012 (October prior to February GUD experiments) and autumn 2013 (concurrent with April GUD experiments) to determine if there were differences in rodent abundance between eight long unburnt and eight recently burnt sites. This included the same 12 sites at which foraging experiments were conducted, plus two additional sites in each fire history (Figure 5.1). Although the October surveys were not concurrent with the GUD surveys, they were still in the same spring–summer activity period and life-history stage of rodent populations at the site, so we do not feel that this represents an issue in data interpretation. Each site had 2 × 60-m aluminium drift fences with six pitfall traps positioned at 10-m intervals along each fence. Traps were open for 10 nights in October and eight nights in April and any captured animals were identified to species, temporarily marked with a non-toxic paint pen and then released at the site of capture. Pitfall trapping is highly effective at catching our target species and has been found to be an effective method for surveying arid-zone rodents in general (Dickman et al. 2011).

Predator abundance

We measured the relative abundance of dingoes and feral cats using 20 Scoutguard 560PV (HCO, China) and 20 Moultrie i60 (EBSCO, Birmingham, Alabama) remote cameras. Cameras were mounted ~30cm above the ground and positioned along vehicle tracks, each separated by at least 2 km and encompassing the same area where rodents were surveyed (Figure 5.1). At half of the camera stations, we used a raw chicken wing encased in a PVC bait holder pegged to the ground as a scent lure and at the remaining cameras we used an electronic device that emitted the sound of a bird tweeting as an audio lure (Lucky Duck, Baldwin, Wisconsin). Lures were swapped between cameras half way through each monitoring period (two weeks in February 2013 and four weeks in May 2013). Cameras were programmed to take three consecutive photographs each time the heat-in-motion sensor was triggered, with a minimum 1-min delay between photo sets.

Research methods followed the American Society of Mammalogists guidelines for use of live animals (Sikes et al. 2011) and were approved by the Edith Cowan University Animal Ethics Committee (permits 8501 and 8875). A field

research permit was issued by the Western Australian Department of Parks and Wildlife (permit SF008871).

Habitat structure

We measured vegetation structure using 2 × 30-m transects at the 16 pitfall trapping sites. At 1-m intervals we counted the number of vegetation touches on a 4-m pole in the following strata: 0–50, 50–100, 100–200, and 200–400 cm above the ground. Every 2 m we measured canopy cover using a spherical densiometer and made visual percentage estimates of bare ground and litter cover in a 50 × 50-cm square.

Statistical analyses

For the GUD data, we used individual tray-nights as data points (Hinkelman et al. 2011) and analysed the two species/groups separately. We excluded data points where neither species/group visited the tray in a night, and data points where both species/groups visited the same tray in a night, because it was not possible to determine which species had visited last. We transformed GUDs to a proportion ('prop-GUD') by dividing values by 20 and used generalized linear mixed models (GLMMs), assuming a binomial error distribution, to assess the influence of fire history and microhabitat on foraging activity. Fire history, microhabitat, and the interaction term were included in the model as fixed effects with two levels per factor: long unburnt and recently burnt, and sheltered and open, respectively. Sampling period (February or April) and the individual tray were specified as random effects to account for variation caused by differences between sampling periods or trays. We report 95% confidence intervals (*CIs*) for the fixed effects and interaction term. Given the complications associated with calculating denominator degrees of freedom and hence performing significance tests in a mixed modelling framework (Pinheiro & Bates 2000), we inferred 'significant' effects where the *CIs* did not overlap zero, which is equivalent to an alpha level of 0.05. The residuals were inspected visually and there were no problematic residual distributions for any of the models. We analysed mixed models using the lme4 package version 1.0-5 in programme R version 3.0.1 (R Core Team 2013; Bates et al. 2014).

We used GLMMs to test the response of rodent species abundance to the fire age of vegetation. To account for differences in sampling effort between seasons, we divided the number of animals caught at a site by the number of nights the traps were open and multiplied this by 100. Fire history was included in the model as a fixed effect (long unburnt or recently burnt) and models were fitted assuming a normal error distribution and using the identity link function. Site and trapping period were specified as random effects in the model to account for variation caused by trapping periods and repeat sampling of sites over time. We calculated 95% *CI*s for fire history and inferred 'significant' differences in abundance where the *CI*s did not overlap zero.

We calculated indices of dingo and cat activity by summing the number of independent photos captured at each camera site in each month. We considered photos of the same species caught on the same camera to be independent when they were captured more than 15 minutes apart. To account for differing sampling effort between months and cameras (e.g. due to battery failure), we calculated a relative abundance index by dividing the number of independent photos taken by each camera by the number of nights it was active and multiplied this by 100. Using ArcMap (ESRI 2012), we calculated the proportion of habitat within a 500-m radius around each camera that was either recently burnt (9–13 years since last fire) or long unburnt (> 40 years). To determine whether dingo or cat activity was related to the fire history of vegetation at a camera site, we fitted GLMMs assuming a normal error distribution with dingo or cat activity as the response variable and the proportion of both long unburnt and recently burnt vegetation as predictor variables. We calculated 95% *CI*s for the predictor variables and inferred 'significant' differences in activity where the *CI*s did not overlap zero.

We used multivariate analysis of variance (MANOVA) to test for significant differences in habitat structure between the two fire histories, with significance set at 0.05. A significant MANOVA was followed by univariate tests to identify which habitat variables differed between fire histories. We logit-transformed proportional variables (litter, bare ground, and canopy cover) and log-transformed pole count data to meet assumptions of normality (Zar 2010).

Results

GUD experiments

GUDs were higher in long unburnt vegetation and in open microhabitat for both *N. mitchellii* and the mouse group (Table 5.1, Table 5.2). The interaction term was significant for the mouse group, but not *N. mitchellii* (Table 5.2). There was no microhabitat effect in long unburnt vegetation for either species/group, but in recently burnt vegetation GUDs were higher in open microhabitat when compared to sheltered for both species/groups (Figure 5.2).

Table 5.1 Mean giving-up densities (number of peanuts remaining) in each combination of microhabitat and fire history treatments. Standard errors are in parentheses.

	<i>Notomys mitchellii</i> <i>n</i> = 247	Mouse group ^A <i>n</i> = 266
Recently burnt, sheltered	14.86 (0.61)	14.79 (0.68)
Recently burnt, open	16.34 (0.59)	16.44 (0.52)
Long unburnt, sheltered	16.38 (0.35)	17.03 (0.30)
Long unburnt, open	16.83 (0.30)	16.55 (0.41)

^A Mouse group, *Pseudomys hermannsburgensis* and *Mus musculus*

Table 5.2 Parameter estimates and 95% CIs for the fixed effects of fire history, microhabitat, and the interaction term on proportional giving-up densities, and the variance estimates for random effects of sampling period and tray. Significant effects (*) were inferred where CIs did not overlap zero. The intercept is the contrast level in the model.

	Model term	Estimate	95% CI
<i>Notomys mitchellii</i>			
Fixed effects	Intercept	1.22	0.71, 1.76
	Microhabitat (open)*	0.75	0.14, 1.37
	Fire history (unburnt)*	0.58	0.02, 1.17
	Microhabitat × Fire interaction	-0.53	-1.36, 0.28
Random effects variance	Tray	0.84	
	Sampling Period	0.03	
Mouse group (<i>Pseudomys hermannsburgensis</i> and <i>Mus musculus</i>)			
Fixed effects	Intercept	1.34	0.82, 1.47
	Microhabitat (open)*	0.75	0.34, 1.18
	Fire history (unburnt)*	0.98	0.74, 1.23
	Microhabitat × Fire interaction*	-0.99	-1.33, -0.65
Random effects variance	Tray	0.69	
	Sampling Period	0.01	

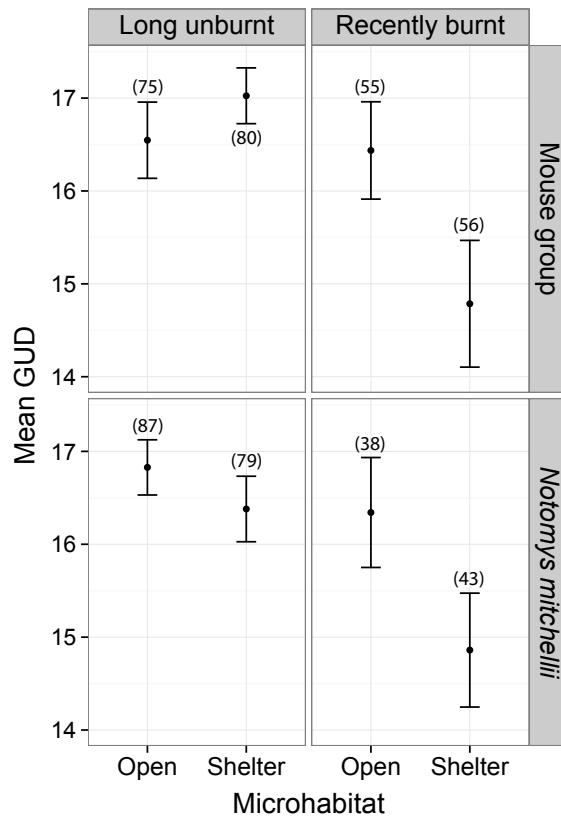


Figure 5.2 Plots of mean GUD values and *SE* bars for the effects of fire history and microhabitat on the ‘mouse group’ (upper panel; *Pseudomys hermannsburgensis* and *Mus musculus*) and *Notomys mitchellii* (lower panel) foraging activity. Sample sizes are in parentheses. GUD, giving-up density.

Rodent abundance

Mean abundance of *P. hermannsburgensis* was 19.22 animals per 100 nights (± 2.93 *SE*), whereas *M. musculus* was 4.77 (± 1.47) and *N. mitchellii* was 7.03 (± 1.83 ; Figure 5.3). There was no difference in abundance between long unburnt and recently burnt sites for *P. hermannsburgensis* (model estimate = -0.31 , *CI* = -9.55 to 8.93), *N. mitchellii* (model estimate = -1.56 , *CI* = -8.21 to 5.09), or *M. musculus* (model estimate = -1.41 , *CI* = -7.25 to 4.43 ; Figure 5.3).

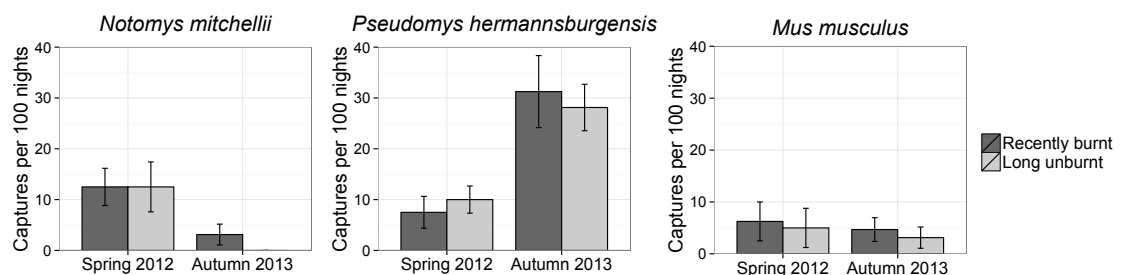


Figure 5.3 Mean and *SE* bars for the abundance of *Notomys mitchellii*, *Pseudomys hermannsburgensis*, and *Mus musculus* in spring (October) 2012 and autumn (April) 2013.

Predator abundance

Mean cat activity was higher than dingo activity in February (cat: 3.36 photos per 100 nights \pm 1.20 *SE*; dingo: 2.19 \pm 0.99) and marginally higher in May (cat: 2.07 \pm 0.40; dingo: 1.88 \pm 0.82). Cat activity was not related to the proportion of recently burnt vegetation (estimate = 1.44, *CI* = -7.85 to 10.73) or long unburnt vegetation at camera sites (estimate = 0.79, *CI* = -8.47 to 10.04), nor was dingo activity (recently burnt: estimate = 0.88, *CI* = -8.06 to 9.82; long unburnt: estimate = 3.59, *CI* = -5.32 to 12.49).

Habitat structure

Mean vegetation density and cover were significantly different between long unburnt and recently burnt sites (Pillai = 0.80, $F_{1,14} = 4.52$, $P = 0.025$).

Univariate tests showed that mean vegetation density at recently burnt sites was 70% higher in the 0- to 50-cm stratum and 35% higher in the 50- to 100-cm stratum when compared to long unburnt sites, whereas vegetation density in the 100- to 200-cm stratum at long unburnt sites was double that at recently burnt sites and was almost 100 times greater in the 200- to 400-cm stratum at long unburnt sites (Table 5.3). Mean canopy cover was almost 10 times higher at long unburnt sites and litter cover was 2.5 times higher, whereas bare ground at recently burnt sites was almost twice that at long unburnt sites (Table 5.3).

Table 5.3 Mean vegetation density (number of touches in each stratum) and percent cover for recently burnt and long unburnt sites and univariate analysis of variance tests for the effect of fire history. Mean variables are untransformed. Significance level is 0.05.

	Recently burnt mean	Long unburnt mean	$F_{1,14}$	P
0-50 cm	2.32	1.36	5.00	0.042
50-100 cm	1.15	0.85	4.69	0.048
100-200 cm	0.63	1.52	13.74	0.002
200-400 cm	0.02	1.75	21.71	< 0.001
Canopy cover (%)	6.82	63.17	28.70	< 0.001
Litter cover (%)	19.00	49.39	22.71	< 0.001
Bare ground (%)	58.45	34.00	19.32	< 0.001

Discussion

Fire history effect

We expected that animals would prefer to forage in the denser, long unburnt habitat rather than in the recently burnt vegetation (hypothesis 1); however, the data did not support this prediction. There are a number of possible explanations for the lower GUDs in recently burnt areas. Firstly, food trays in recently burnt habitat may have been perceived as more valuable if background levels of food availability were lower and competition was higher in recently burnt habitat (Davidson & Morris 2001; Ylönen et al. 2002). Individuals living in a resource poor environment can be more likely to undertake risky foraging behaviour compared to those in resource rich environments (Olsson et al. 2002). If this was the case, we would expect GUDs to be lower in both the sheltered and open microhabitats in recently burnt compared to long unburnt areas. Although we did not measure food availability, this seems unlikely to be a significant explanatory variable because GUDs were only lower at sheltered trays in recently burnt areas, whereas open trays in recently burnt areas were similar to both sets of trays at long unburnt sites.

Alternatively, lower GUDs in recently burnt areas may occur if predator abundance and hence predation risk were lower there. However, there is little support for this idea, since remote camera monitoring showed that cat and dingo activity during the study period were similarly high irrespective of the amount of long unburnt or recently burnt vegetation around camera sites. These indices are able to provide data on the relative abundance of predators across the landscape; however, we acknowledge that they do not provide information on fine-scale movements or hunting strategies within different habitat types. Although difficult to obtain, direct measurements of the number of prey killed by predators in each habitat type could provide information on the actual predation pressure experienced in these different areas. Based on the data available, the observed pattern appears to be related to differences in the vertical distribution of vegetation structure and is linked to our third hypothesis, which we discuss later.

Microhabitat effect

GUDs were higher in open microhabitat, which supports our second hypothesis. Use of complex microhabitats in this study suggests that rodents are using risk-averse behaviour by foraging in sheltered microhabitats to avoid encounters with predators and reduce their chance of being depredated. Indeed, cats are known to prey on all three species at the study site and were common during the study period (Chapter 3), which suggests that they presented a genuine threat to the rodents studied here. The reduced foraging activity in open areas is consistent with the notion that animals perceive a greater predation risk in open areas since predator encounters are generally more likely to occur in the open (Kotler et al. 1988; Dickman et al. 1991; Janssen et al. 2007). In Australia's Simpson Desert, *P. hermannsburgensis* and *N. alexis* prefer to forage in complex microhabitats during periods of high predator activity (Dickman et al. 2010b) and on Australia's Fraser Island, rodents reduced their foraging activity following experimental reduction of cover (Spencer et al. 2005). Stokes et al. (2004) also found that two dasyurid marsupial species had lower GUDs under artificial cover than in open habitats and inferred that this was due to predation risk. Risk-sensitive foraging behaviour by rodents can vary with temporal changes in predator activity (Dickman et al. 2010b; Dickman et al. 2011), so future studies in this system could compare the use of sheltered and open microhabitats during times of low and high predator activity.

Combined effects of microhabitat and fire history

Our results showed no effect of microhabitat in long unburnt areas, but clear differences between sheltered and open microhabitat in recently burnt areas. We expected GUDs to be lower overall in long unburnt areas and that microhabitat would be less important there because the taller and denser vegetation would impair visual detection of prey by predators and hence negate the need for additional refuge while foraging. However, our rejection of hypothesis 1 indicates that this may not be the case, since overall, GUDs were actually higher in long unburnt areas.

The absence of a microhabitat effect in long unburnt areas suggests that the study species perceive a similarly high predation risk when foraging at sheltered and open patches in long unburnt areas. This pattern appears to be related to the

density of vegetation structure close to the ground, rather than in the canopy. Our vegetation measurements confirm the findings of previous studies that canopy cover increases and becomes more continuous with increasing time since fire in *Acacia* shrublands, whereas ground-level vegetation cover decreases, and the density of short shrubs in long unburnt areas is lower than that in recently burnt areas (Parsons & Gosper 2011; Dalgleish et al. 2015). Since the feral cat is a major predator of the study species and cats were common during the study period, it is intuitive that vegetation density in the lower stratum is more important than canopy cover in mediating predation risk. Sheltered microhabitats are expected to decrease predation risk for these small mammals by providing vegetation cover that hinders visual detection by predators and provides shelter to escape to when threatened. Consequently, foraging in areas with dense vegetation close to the ground (e.g. areas 9–13 years since last fire) likely provides the rodents in our study system with improved survival rates (Torre & Díaz 2004).

Conservation and management implications

Our findings have revealed that shrubland fire history can have a significant impact on the foraging behaviour of small rodents. An unexpected finding was that rodents spent more time foraging in recently burnt rather than long unburnt areas. Vegetation patches in intermediate fire ages provide rodents with refuge and hence are likely to aid the persistence of rodents in these areas. However, the vegetation here has recovered over 9–13 years since being burnt and younger post-fire ages (e.g. 0–3 years) are likely to present small mammals with greater predation risk since vegetation cover is greatly reduced immediately following a fire (Conner et al. 2011). Younger post-fire ages were not available at the time of this study.

Although further studies across a wider range of fire ages will provide greater clarity, results from this and other studies suggest that a range of post-fire successional stages should be maintained across such landscapes to conserve small mammal communities (Horn et al. 2012; Kelly et al. 2012; Chapter 4). Inappropriate fire regimes threaten small mammal communities in Australia (Woinarski et al. 2014) and elsewhere globally (Kelt & Meserve 2014; Plavsic 2014) and future increases in fire extent and severity in Australia will increase loss of protective cover and hence potentially exacerbate the impact of introduced

predators like feral cats and foxes on small mammals (Woinarski et al. 2011; Conner et al. 2011; Radford et al. 2014). If the negative impacts of introduced predators and inappropriate fire regimes are to be reduced, land management actions must consider the behavioural, as well as population-level responses of small mammal communities to differing fire regimes.

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Chapter 6.

Synthesis and conclusions

In this thesis I examined relationships between the fire history of shrublands, and the ecology of feral cats and their prey and competitors. Although the work was conducted in the semi-arid northern Wheatbelt region of Western Australia, the results have broader implications for the management of feral cats in other parts of Australia and elsewhere globally. I first reviewed the literature, aiming to identify general patterns in habitat use by feral cats and the major factors driving these patterns. Secondly, I applied this framework to a field study of habitat selection by feral cats with regard to the fire history of shrublands and I also studied overlap in resource use between sympatric cats and dingoes. Thirdly, I studied patterns of habitat selection by small mammals and reptiles that cats prey on. Lastly, I undertook field experiments to examine whether small rodents altered their risk-sensitive foraging behaviour in different shrubland fire ages.

In this final chapter, I first summarise the key findings of this body of work in relation to the thesis objectives. I then provide a synthesis of the results and discuss how these findings can be applied to invasive predator management. Finally, I present a new framework for conceptualising interactions between invasive predators and other ecological disturbances (e.g. fire).

Summary of major findings

Objective 1: Critically review the literature to identify the primary factors influencing feral cat habitat use.

My review of feral cat habitat use revealed that cats inhabit a very wide range of ecosystems across the globe, including arid deserts, shrublands and grasslands, fragmented agricultural landscapes, urban areas, glacial valleys, equatorial to sub-Antarctic islands and a range of forest and woodland types. Three general patterns emerged:

- (1) cats were generally recorded most often in habitat types characterised by a mixture of plant growth forms close to ground level, rather than those with an open or homogenous structure;

(2) cats were more likely to be recorded at the edges of vegetation patches, or along linear features such as road verges or creeks that traversed patches, than in the patch interior; and

(3) it is hypothesised that cats behaviourally stratify their habitat use; i.e. certain habitats are used for shelter or resting, and others for hunting.

Not all studies conformed to these patterns though and generality is difficult to draw out here due to the behavioural plasticity of cats, the small number of studies available and the range of different study designs and techniques used. Despite their wide-ranging impacts on biodiversity across the globe, only 27 studies of cat habitat use were suitable for review and the strength of evidence contained within them was generally low. Most studies were observational or correlative and hence were unable to distinguish between multiple confounding factors potentially influencing the observed patterns. My own field study on this topic experienced similar shortcomings (Chapter 3). Stronger inferences regarding habitat use and selection by cats will be gained through the use of replicated manipulative experiments conducted at the landscape scale. Only one published study used such an approach, which is understandable given the resources and spatial scale necessary for such investigations. Based on the conceptual model presented in Chapter 2, I developed three testable hypotheses regarding habitat use by cats:

(1) higher-order predators with a high dietary overlap with feral cats and strong competitive ability will have spatially or temporally prohibitive effects on cat habitat use (Heithaus 2001; Wilson *et al.* 2010; Ross *et al.* 2012);

(2) where higher-order predators exclude feral cats from using areas with optimal prey availability, removal of those predators will allow cats to expand their use of optimal prey habitat (Molsher 1999; Prugh *et al.* 2009; Ritchie and Johnson 2009); and

(3) prey and/or shelter availability will be the most important factors influencing cat habitat use where higher-order predators are absent (Heithaus 2001).

The resolution of data being collected on carnivore spatial ecology is already increasing rapidly with the advent of new remote sensing, GPS tracking and motion-sensing camera technologies, although technology is no substitute for good experimental design. High-resolution data on predators, prey and competitors paired with sound study design will improve our understanding of habitat use by feral cats and other invasive predators, and help reduce their impacts on threatened species.

Objective 2: Examine how the fire history of vegetation influences habitat selection by cats.

Using remote cameras, I examined habitat selection by cats with regard to the fire history of shrublands and discussed the findings in relation to prey availability and the competitive influence of dingoes (*Objective 3*). Cats were recorded in all four major habitat types: recently burnt shrublands (10 to 14 years since last fire), long unburnt shrublands (34 to ~49 years), very long unburnt shrublands (> 50 years), and woodlands. Cats were recorded most frequently in the north of the reserve and in areas dominated by very long unburnt shrublands. The candidate explanations for these patterns were: higher rabbit availability in the north of the reserve, heterogeneous habitat structure in very long unburnt shrublands providing improved hunting success, and/or coincidence due to low cat numbers in the south of the reserve where very long unburnt shrublands were less common. My ability to distinguish between these explanations was limited by the study design. Future studies will benefit from using a more integrated strategy that surveys predators, prey and competitors simultaneously in different habitat types and at different times of the year.

Objective 3: Investigate overlap in resource use between sympatric cats and dingoes.

I examined overlap in resource use between cats and dingoes using remote camera surveys and dietary analysis of scats. The diet of feral cats was more diverse than that of dingoes, with cats consuming 11 mammal species and dingoes six. Dietary overlap between the two carnivores was relatively low, although few studies were available for comparison. Rabbit remains occurred relatively frequently in both cat and dingo scats, but small mammals, reptiles and birds were also common in cat scats, and macropods in dingo scats. Dingoes showed a preference for woodlands, whereas cats preferred very long unburnt shrublands.

Cats were recorded at nearly half the sites where dingoes were also recorded during the same session. Mean diurnal activity time for feral cats was two and a half hours later than that of dingoes. Nonetheless, the relative infrequency of dingo records throughout the study limits the conclusions that can be made regarding any competitive influence they may have on cat habitat use.

Objective 4: Identify patterns of prey habitat selection to assess whether some species are at a greater risk of predation due to habitat selection by cats.

I used pitfall trapping to determine whether small mammals and reptiles that cats prey on exhibit preferences for either recently burnt or long unburnt shrublands. Nine of the 15 study species showed such a preference, with two small mammals and three reptiles being most abundant in recently burnt areas and one small mammal and three reptiles being most abundant in long unburnt areas. Aside from cat predation (discussed under *Synthesis*), the preference of some species for certain fire ages highlights their potential vulnerability to changing fire regimes. Both uncontrolled fires and fire management that homogenises large areas of habitat through either fire exclusion or frequent burning may threaten species that specialise in distinct post-fire stages (Smith et al. 2013). In the study area, those species in longer unburnt areas are most at risk because only ~25% of the shrublands remain unburnt and they take several decades to recover once burnt (Dalglish et al. 2015).

Objective 5: Determine whether fire-induced changes in habitat structure influence the behaviour of cat prey species.

I used giving-up density experiments to examine risk-sensitive foraging behaviour by rodents in two shrubland fire ages and microhabitats. The rodents foraged for longer in sheltered compared to open microhabitats, but this pattern only occurred in recently burnt, not long unburnt shrublands. I proposed that this occurred because the higher density of understorey vegetation in recently burnt areas provided the rodents with extra cover to hide and escape from predators, whereas the understorey vegetation is less dense in longer unburnt areas, hence providing rodents with less protection.

Synthesis

Throughout this thesis I have examined predator-prey ecology in a shrubland system where fire is an important landscape modifier. Overall, cat activity was highest in areas of very long unburnt shrublands, although early in the study their activity was equally high in recently burnt shrublands. This suggests that both young and old fire ages can provide suitable habitat for cats at least sometimes. The response of feral cats and other invasive predators to variable fire regimes has been poorly studied. McGregor *et al.* (2014) showed that cats in tropical north-western Australia preferentially hunted in grasslands that had recently been grazed or intensely burnt and posited that this was because of the improved hunting opportunities these areas provided. Pastro (2013) found that foxes and cats occurred more frequently on ecotones between burnt and unburnt grasslands when compared to continuous habitat. Although at a broader scale, Payne *et al.* (2014) found that foxes were widely distributed in the mallee region of south-eastern Australia, irrespective of fire age. Other studies have recorded preferences for burnt areas by small and medium-sized carnivores, including the striped skunk *Mephitis mephitis* and gray fox *Urocyon cinereoargenteus* in North America (Borchert 2012; Schuette *et al.* 2014), and dogs *Canis lupus familiaris* and red foxes in the Mediterranean (Birtsas *et al.* 2012). It is important to acknowledge that it isn't fire *per se* driving these patterns, but rather fire-induced changes in vegetation structure that make certain areas more or less profitable habitat for the carnivores. This profitability is likely to change as vegetation recovers post-fire (e.g. Torre & Díaz 2004), therefore the patterns I recorded here may have differed if an immediate post-fire age (e.g. < 3 years) was sampled. No such areas were available during the study and future fires in the area will provide valuable opportunities to assess the immediate post-fire responses of both predators and prey. The observed patterns also varied between sampling sessions and these observations highlight the importance of incorporating both seasonal and successional temporal scales into studies of carnivore space use.

Such temporal changes in habitat suitability are not limited to just fire, but extend to other processes such as logging (Colón 2002; Godbout & Ouellet 2008) and livestock grazing (Villar *et al.* 2013; McGregor *et al.* 2014). Given the prevalence of cats, fire, grazing and logging in many biomes worldwide, many feral

cat control programmes are likely to benefit from acknowledging how temporal changes in vegetation cover influence predator populations and hence their management. For example, control of cats could be timed to coincide with planned burns to alleviate an expected spike in predation pressure (Conner et al. 2011; Leahy 2013). Provision of artificial refuges may also provide prey species with additional protection (Arthur et al. 2005), although their efficacy should be assessed experimentally (Lettink et al. 2010). Management of other invasive predators, such as red foxes and American mink *Neovison vison*, is also likely to benefit from such approaches.

The higher cat activity in very long unburnt shrublands suggests that the four mammal and reptile species that were most abundant in long unburnt areas may be at higher risk of predation by cats. Interestingly, the scat analysis lends some support to this idea. Capture rates of the fat-tailed dunnart *Sminthopsis crassicaudata* were more than three-fold higher in recently burnt compared to long unburnt shrublands, whereas the little long-tailed dunnart *S. dolichura* showed the opposite trend, i.e. capture rates in long unburnt shrubland were twice those in recently burnt areas. *Sminthopsis dolichura* was identified in 4% of cat scats, whereas *S. crassicaudata* was not identified in any scats, which supports the notion that *S. dolichura* would experience higher predation rates by virtue of being most abundant in longer unburnt areas where cats are more common. It is possible, however, that *S. crassicaudata* was present in the 4.9% of cat scats containing *Sminthopsis* remains that could not be identified to the species level. Also, the above ideas are based on the implicit but likely untrue assumptions that cats only hunt in shrublands or that the dunnarts only inhabit shrublands. Extrapolation of the observed patterns of prey habitat selection from long unburnt to very long unburnt areas is supported by studies showing that the vegetation structure of these two fire ages is most similar compared to younger fire ages (Dalglish et al. 2015). Due to the nature of scat analysis, few reptiles were identified to the species level, hence it is not possible to make inferences here regarding higher/lower rates of predation based on their habitat preferences.

Very few studies have assessed small mammal foraging behaviour in response to fire-induced habitat changes (Spencer et al. 2014a), however, I have shown that the rodents studied here exhibited differential foraging activity

between shrubland fire histories, with microhabitat apparently mediating predation risk in young but not old shrublands. The fact that the abundance of the rodents did not differ between the two fire histories, but their foraging behaviour did, highlights the importance of considering behavioural, as well as population-level responses of small mammals to differing fire regimes. The role of fire in predator-prey dynamics is particularly interesting because global climate models predict increases in fire frequency and intensity in some parts of the world (Pechony & Shindell 2010), and such changes may also arise due to increased rates of prescribed burning by land managers attempting to reduce the risk of large wildfires (Penman et al. 2011). Given the role that fire-induced changes in vegetation structure can have in shaping both small mammal behaviour and population dynamics, further research is needed to understand and predict how small mammal communities will respond to altered fire regimes into the future, especially where the effects may be compounded by invasive predators.

Studies from Australia's Simpson Desert have shown that *Pseudomys hermannsburgensis* alters its foraging behaviour according to temporal changes in predator abundance, i.e. mice are more risk-averse when predators are more common (Dickman et al. 2010b; Dickman et al. 2011). I conducted the foraging experiments when cat activity was similar between the northern and southern camera circuits, although repeating the experiment following the decline in cat activity on the southern circuit may have produced different results. Based on the model that rodents are less risk-averse during times of low predator activity, I predict that the effect of microhabitat in recently burnt shrublands would be observed at the northern sites where cats were common, but not on the southern sites where cats were scarce. This is because the lower predation risk would negate the need to preferentially forage under cover. Future studies could also assess the length of time it takes for prey species to alter their behaviour following changes in predator abundance. The potential for prey species to alter their behaviour according to seasonal conditions again highlights the value of incorporating temporal information into studies of predator-prey dynamics.

New conceptual framework³

Management of invasive predators is a central conservation goal globally and is usually attempted through lethal control, such as baiting, trapping or shooting. These programmes have at times been successful in reducing predation pressure on native prey (e.g. Robley et al. 2014), however, they are extremely costly (Zuberogoitia et al. 2010) and their applicability at larger scales is questionable (Lieury et al. 2015). These approaches also often fail to consider the density-independent impacts of predators ('functional' impacts, defined below), nor how they might interact with other threatening processes operating at the same time. This has led to unpredictable outcomes of invasive predator control; sometimes it is ineffectual (Bodey et al. 2011; Lazenby et al. 2014), or worse, results in a net negative outcome for biodiversity (Norbury et al. 2013; Marlow et al. 2015). This suggests an urgent need to refine our understanding of invasive predator management, such as when and where to use lethal control, and to consider alternative means of reducing the impact of invasive predators on native biodiversity aside from lethal control.

Here, I present a new framework built around six widespread and important threats with strong potential to interact with invasive predators and their control: land clearing, altered fire regimes, large herbivore grazing, anthropogenic resource subsidies, altered prey populations, and the loss of top-predators (Figure 6.1). These six threats can be classified as belonging to one of two categories reflecting their underlying ecological cause: those that are mediated by alterations in vegetation structure ('habitat-mediated threats') and those that arise due to the composition of the fauna community ('community-mediated threats') (Figure 6.1).

³ This section is adapted from the following paper of which I am the lead author: Doherty TS, CR Dickman, DG Nimmo and EG Ritchie (2015) *Multiple threats, or multiplying the threats? Interactions between invasive predators and other ecological disturbances*. *Biological Conservation*, 190:60–68.

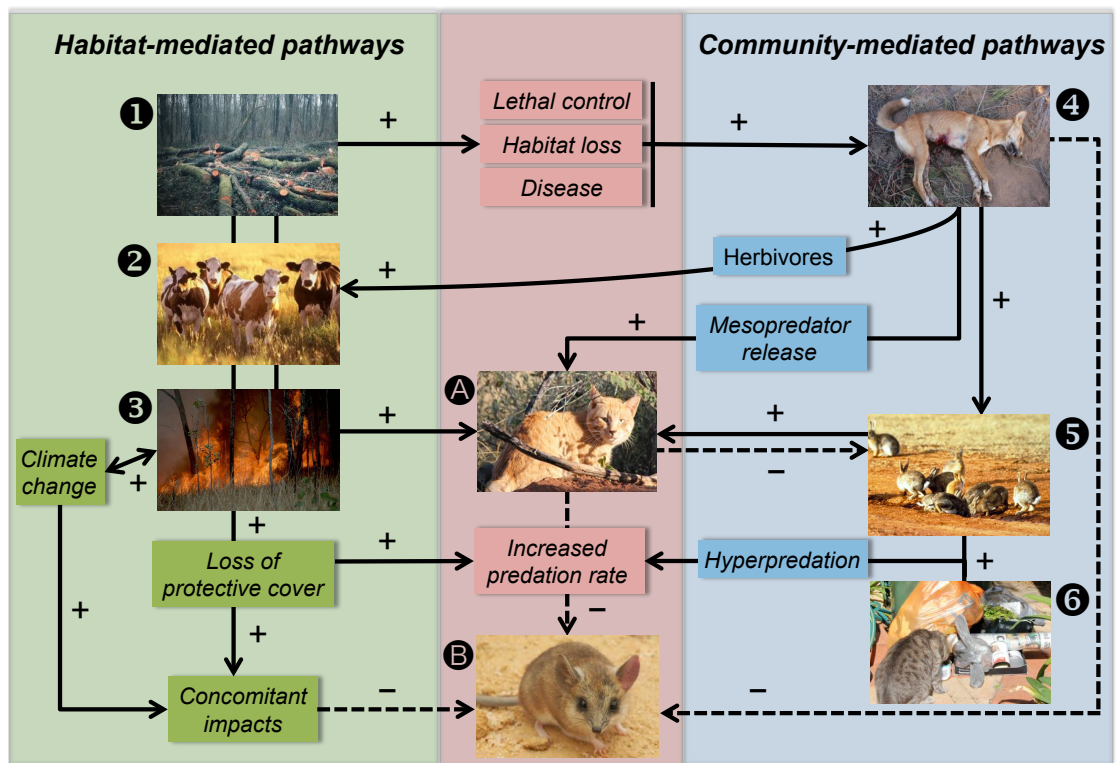


Figure 6.1 Conceptual model of the relationship between community- and habitat-mediated interaction pathways and their effects on native fauna. Habitat-mediated interaction pathways are processes that modify the structure or integrity of habitat and in turn exacerbate the impacts of invasive predators (A) on native fauna (B). Community-mediated interaction pathways are changes in the presence or abundance of a top-predator or its prey species that can lead to increased population densities or altered behaviour of invasive predators that in turn exacerbate their impacts on native fauna. The primary threats interacting with invasive predators are: (1) land clearing; (2) grazing; (3) fire; (4) top-predator decline; (5) altered prey populations; and (6) anthropogenic resource subsidies. Additional processes are indicated with italicised text. Solid lines represent positive effects (+) and dashed lines represent negative effects (-). Image credits: 1, endymion120 (Flickr, CC BY 2.0); 2, USDA (public domain); 3 & 5, CSIRO (CC BY 3.0); 4, 6, A & B, T. Doherty.

Central to this synthesis is the notion of interactions between disturbances, both additive and synergistic (Didham et al. 2007; Brook et al. 2008). Additive effects of disturbances occur when two disturbances that overlap in space and time combine to impact an ecological response variable in a way that is equal to the summing of their independent effects. For example, if land clearing and invasive predators each reduce the population size of a native mammal by 20% in isolation, then populations subject to both land clearing and invasive predators

will have a population reduction of 40%. By contrast, synergistic effects arise when two disturbances that overlap in space and time have an impact greater than the sum of their independent effects. Thus, considering the above example, if the combination of land clearing and invasive predators resulted in a 60% decline of the mammal population, the additional 20% above their respective effects represents a synergy. Today, most ecosystems are subject to multiple disturbances that operate at various spatial and temporal scales and interact to some degree, either additively or synergistically (Didham et al. 2007; Brook et al. 2008; Anson et al. 2014).

With regards to invasive predators, there are at least three situations where synergistic impacts are likely to occur. Two of these relate to the response of invasive predators themselves to an ecological disturbance (Didham et al. 2007). First, a disturbance may increase the abundance of an invasive predator by improving habitat amount and/or quality. For example, modified landscapes in Australia support higher abundances of introduced red foxes compared to intact areas (Towerton et al. 2011; Graham et al. 2012). An increase in the abundance of an invasive predator will in many cases lead to an increase in its impact on native fauna, and this represents a 'numerical' impact of invasive predators (Didham et al. 2007). Second, a disturbance may increase the *per capita* impact of invasive predators. That is, although the invasive predator's population density may remain stable, there is a shift in behaviour such that native fauna are more likely to be depredated when invasive predators co-occur with the threat. For example, predation rates of hispid cotton rats *Sigmodon hispidus* increased following prescribed fire in Georgia, USA (Conner et al. 2011). This is a 'functional' impact of invasive predators, as their impact on native prey populations is independent of their population density (Didham et al. 2007). Third, where the concomitant threat itself strongly affects a native species' population, invasive predators may exacerbate its effects such that the loss of individuals from the population due to predation has disproportionate impacts on the population and its rate of decline (e.g. Allee effects) (Soulé et al. 1988).

Fire and predation: a case in point

Fire is one of the most widespread ecological disturbances globally (Bowman et al. 2009) and can allow predators improved access to structurally complex habitats (Birtsas et al. 2012; McGregor et al. 2014), thereby potentially facilitating functional impacts on prey. Birtsas et al. (2012) found that visitation rates of foxes and dogs *Canis lupus familiaris* at sampling stations in an intensely burned area were greater than in both a moderately burned area and an unburned area. Pastro (2013) found that foxes and cats occurred more frequently on ecotones between burnt and unburnt grasslands when compared to continuous habitat. Fire can also lead to increases in local predator occurrence, thereby leading to potential numerical effects (Borchert 2012; Schuette et al. 2014).

Increases in predation rates of small mammals following fire (Conner et al. 2011; Leahy 2013) support the notion of both functional and numerical impacts. Christensen (1980) recorded high rates of fox predation on a threatened marsupial soon after fire in south-western Australia, and Wayne et al. (2006) hypothesised that a negative relationship between possum abundance and fire intensity arose because fire caused possums to spend more time on the ground and predators were attracted to areas of disturbance, hence making possums more vulnerable to predation. In support of this, feral cats preferred to hunt in recently burnt or grazed grasslands in northern Australia (McGregor et al. 2014).

Fire can cause direct mortality of prey (Hailey 2000; Smith et al. 2012b), and may lead to population reductions due to changes in resource availability (Sutherland & Dickman 1999). Fire therefore represents a compounding threat. A key mediating factor in the interaction between fire and predation is the availability of refuges for prey species (Torre & Díaz 2004; Robinson et al. 2013). Native rodents in north-western Australia experienced greater predation by feral cats in a high intensity fire treatment, compared to a low intensity, patchy burn and an unburnt control (Leahy 2013). In semi-arid mallee shrublands, the post-fire response of a range of small mammal and reptile species is dependent on the availability of structurally complex spinifex hummocks (Kelly et al. 2011; Nimmo et al. 2012b), potentially because of their role in providing protection from predators (Cogger 1974). These hypotheses suggest that fire-induced changes in vegetation structure change the availability of protective cover, and hence alter the

vulnerability of prey to predation. If the provision of refuges is important to reducing predation pressure, lower intensity fires that retain patchiness should reduce the predation-related impacts of fire on native species. This area will benefit from further experimental work that assesses the relative importance of numerical and functional impacts in post-fire environments. Interactions between fire and predation are likely to be further exacerbated by future increases in fire frequency and intensity that are predicted in global climate models (Pechony & Shindell 2010), or by increased rates of prescribed burning (Penman et al. 2011).

Concluding remarks

Ameliorating interactions between invasive predators and other disturbances presents conservation practitioners with a considerable challenge, not least because of the wide range of ecosystems in which these interactions operate. This framework provides a gateway for rethinking conventional approaches to invasive predator management. Conservation practitioners must identify and address habitat- and community-mediated interaction pathways if these impacts are to be reduced. Given that these processes are largely driven by human influences, implementation of appropriate land management practices should help reduce invasive predator impacts. Such approaches include improved management of fire and grazing, integrated multi-species pest management and conservation of top-predators (Doherty et al. 2015). Rather than focussing on single processes, effective management of invasive predators requires explicit acknowledgement of the multiple threats operating in stressed ecosystems and use of management actions that address these factors in unison. Such integrated approaches are essential if further extinctions and their cascading effects are to be avoided.

Appendix A.

A continental-scale analysis of feral cat diet in Australia

Doherty TS, RA Davis, EJB van Etten, D Algar, N Collier, CR Dickman, G Edwards, P Masters, R Palmer and S Robinson (2015) *A continental-scale analysis of feral cat diet in Australia*. *Journal of Biogeography*, 42:964–975.

Introduction

Invasive mammalian predators are a global threat to biodiversity (Salo et al. 2007). Species like the red fox *Vulpes vulpes* (Johnson 2006), some rats *Rattus* spp. (Jones et al. 2008; Capizzi et al. 2014) and the domestic cat *Felis catus* (Dickman 1996b; Medina et al. 2011; Duffy & Capece 2012) have caused numerous declines and extinctions of native species worldwide. The domestic cat is a medium-sized carnivore occupying a range of habitats across a broad global distribution (Turner & Bateson 2000). Humans keep cats as companion animals, but cats also live in self-sustaining feral populations in urban and non-urban areas (Turner & Bateson 2000). Feral cats have contributed to at least 14% of bird, mammal and reptile extinctions on islands globally (Medina et al. 2011), including those of 16 mammals in Australia⁴ (Johnson 2006), and have caused the failure of numerous reintroduction attempts for threatened mammal species (Christensen & Burrows 1994; Gibson et al. 1994; Potts et al. 2012). Reducing the harmful impact of feral cats is a priority for conservation managers across the globe (Daniels et al. 2001; Medway 2004; Woinarski et al. 2011; Loss et al. 2013; Nogales et al. 2013), and success in achieving this aim requires a detailed understanding of feral cat ecology across a broad spectrum of climatic and environmental conditions.

The feral cat is ubiquitous in Australia and occurs on many of its territorial islands: it inhabits deserts, savanna grasslands, urban and agricultural lands, temperate and tropical woodlands, and other areas (Denny & Dickman 2010). It

⁴ This number has since been revised to 22 by Woinarski *et al.* (2015) to reflect taxonomic changes and other new information.

feeds on small- and medium-sized mammals, as well as reptiles, birds, arthropods, frogs and carrion (Denny & Dickman 2010). Cats are considered to be a contributing factor to recent declines in northern Australia's mammal fauna (Woinarski et al. 2011; Fisher et al. 2014a) and are listed as a *Key Threatening Process* under the Commonwealth *Environment Protection and Biodiversity Conservation Act 1999* (Department of the Environment Water Heritage and the Arts 2008). Reducing their impact is considered to be an essential action for the conservation of Australian birds and mammals (Woinarski et al. 2011; Garnett et al. 2013; Woinarski et al. 2014).

Feral cats are opportunistic and generalist carnivores that use food resources in proportion to their availability (Jones & Coman 1981; Fitzgerald 1988). Landscape context can have a strong influence on cats' diets at local or regional scales in Australia (Coman & Brunner 1972; Martin et al. 1996) and prey abundance and distribution also influence the space use and movements of cats (Turner & Meister 1988), but the higher-order effects of habitat type, climate and other geographical factors such as productivity on the dietary composition of feral cats in Australia, and elsewhere, remain largely unknown. Such an analysis is essential to understanding cat impacts at a broad scale and to provide an informed framework for management action.

Biogeographical dietary studies of the feral cat on islands worldwide (Bonnaud et al. 2011), and on the closely related wildcat *Felis silvestris* in Eurasia (Lozano et al. 2006), have found that consumption of reptiles and invertebrates is greatest at lower latitudes. This perhaps reflects the greater species richness of these groups at lower latitudes (Schall & Pianka 1978). The frequency of the European rabbit *Oryctolagus cuniculus* in the diet of medium-sized carnivores is largely dependent on the abundance of rabbits in the local landscape; these carnivores feed preferentially on rabbits when they are available, but will switch to small rodents in areas where – or at times when – rabbits are less abundant (Malo et al. 1999; Lozano et al. 2006; Díaz-Ruiz et al. 2011). Rabbits in Australia show seasonal fluctuations in abundance and are absent from most of northern Australia above 21°S because of environmental constraints on their survival (Williams et al. 1995; West 2008). Consequently, Australian feral cats could be expected to adopt a

strategy similar to that of other medium-sized carnivores of switching between rabbits and small mammals depending on availability.

In this study, we analyse the diet of the feral cat across its geographical range in Australia and on Australian territorial islands, seeking to identify biogeographical patterns in dietary composition and diversity and we use the results to consider how feral cats may best be managed. Based on the general model that cats are primarily generalist and opportunistic carnivores that show some preference for rabbits, we test the following hypotheses concerning the diet of feral cats:

- (1) Reptile consumption will be correlated negatively with mean annual rainfall and will be highest in arid regions where species richness of reptiles is greatest (Schall & Pianka 1978; Powney et al. 2010);
- (2) Arthropod and reptile consumption will be higher at lower latitudes (i.e. closer to the equator) (Lozano et al. 2006; Bonnaud et al. 2011; Díaz-Ruiz et al. 2011); and
- (3) Small mammal consumption will be correlated negatively with rabbit consumption (Malo et al. 1999; Lozano et al. 2006; Díaz-Ruiz et al. 2011).

In assembling the data sets needed to test these hypotheses, we also comment on the range of prey species that are killed by feral cats in Australia.

Materials and methods

We searched Web of Science and Scopus databases for studies on the diet of feral cats in Australia, using combinations of the following keywords: cat, feral cat, *Felis catus*, diet, predation, ecology and Australia. We sourced additional studies from reference lists, book chapters, publicly available theses and reports, and unpublished data collected by the authors of this paper. Data collation occurred between June 2013 and March 2014 inclusive. A full list of references is given in Table B.1 in Appendix B.

The sampling units used in these studies were scats and stomach contents. The criteria for including a data set were: (1) the study animals were unambiguously feral cats in Australia or its territorial islands, not pet or stray cats;

(2) data were recorded as the frequency of occurrence (FO) of food items or could be converted to this metric [i.e. the proportion of sample units in a study (stomachs or scats) that contain a type of food]; (3) sample size was ≥ 20 scats and/or stomachs from a site; and (4) data were collected during all seasons of cats' activity (i.e. at least one entire year). We excluded two studies where the diet of cats was heavily subsidized by food scavenged from refuse sites (Hutchings 2003; Denny 2005).

Data on food volume, biomass or relative frequency are considered the most suitable metrics for inter-population studies (Klare et al. 2011). However, like earlier authors (Klare et al. 2011; Díaz-Ruiz et al. 2011), we found that few studies used any one of these measures. The percentage frequency of occurrence (%FO) was the most consistently used measure and is considered a valid metric for comparison between different studies (Klare et al. 2011). We therefore gathered data on the %FO of different dietary components. After screening all studies through our inclusion criteria, we included 49 data sets in our analyses (see Table B.2 in Appendix B).

We defined eight food categories: arthropods (spiders, scorpions, centipedes, millipedes, insects); reptiles; birds; dasyurid marsupials (< 500 g mean adult body weight; Dasyuridae); rodents (< 500 g; Muridae); native medium-sized mammals (500–6,999 g); European rabbit *Oryctolagus cuniculus*; and carrion. In the carrion category we pooled anything reported as 'carrion' with any data on camels *Camelus dromedaries*, emus *Dromaius novaehollandiae*, large macropods (*Macropus* species $\geq 7,000$ g) and livestock (cattle, goats, sheep and pigs), assuming that these large-bodied prey items would most likely have been eaten only as carrion. If a study provided data for multiple species within a food category, but not a group value, we took the value of the most frequently occurring species as the group value, which is the minimum possible FO for that group, and is thus a conservative estimate. If a study contained separate seasonal values but not overall values, we averaged data across all seasons.

Statistical analyses

We compiled an inventory of every vertebrate species and invertebrate group recorded as eaten or killed by feral cats in Australia based on information in

the dietary studies, as well as other published accounts of cat predation such as records of cats killing translocated mammals (e.g. Gibson et al. 1994; Moseby et al. 2011b). We calculated study duration by counting the number of months between the start and end of collection periods. Study duration could not be calculated for one study (Mahood 1980). We classified data sets according to the following climate-habitat regions: south-western shrublands, woodlands and forests (SW); tropical and sub-tropical grasslands, savannas, shrublands and forests (TROP); deserts and xeric shrublands (ARID); eastern inland shrub/grass/woodlands and savannas (EAST); south-eastern temperate forests and heath (SE); and islands (ISL; Figure A.1). These groups are based on a modified version of the Terrestrial Ecoregions of the World system (Olson et al. 2001): the Mediterranean east is split from the Mediterranean south-west (SW) and then combined with the 'temperate grasslands, savannas and shrublands' region to create the EAST region. Additionally, tropical and subtropical regions are combined (TROP), montane areas are subsumed into the surrounding SE region and all islands are classified as ISL irrespective of location, except for the very large island of Tasmania. These modifications are based on regional environmental correlates such as rainfall and vegetation type and yield an ecologically relevant set of regions that are not so numerous that only a few studies are represented in any single region.

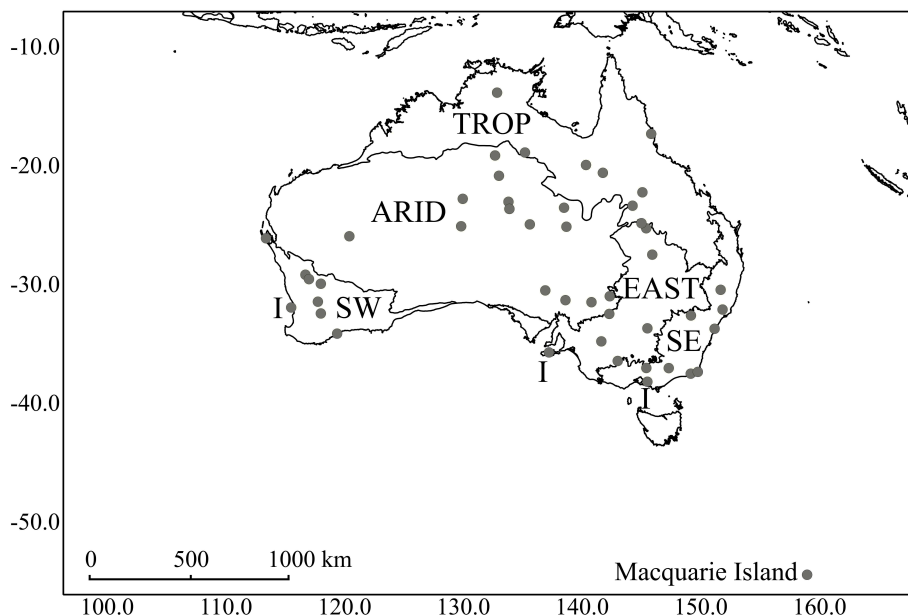


Figure A.1 Study locations and climate-habitat regions. ARID, deserts and xeric shrublands; EAST, eastern inland shrub/grass/woodlands and savannas; I, islands; SE, south-east temperate forests and heath; SW, south-west shrublands, woodlands and forests; TROP, tropical grasslands, savannas, shrublands and forests.

For each data set we recorded the latitude and longitude (decimal degrees) to two decimal places and extracted WORLDCLIM data for mean annual precipitation (mm) and mean annual temperature (degrees Celsius \times 10) from the Atlas of Living Australia database (available at <http://spatial.ala.org.au/>). The environmental productivity of each study location was inferred from the normalized difference vegetation index (NDVI) using monthly remotely sensed NDVI averages for the period 1980–2010 at a resolution of 0.05° (see the Vegetation Index and Phenology Lab, University of Arizona, available at <http://vip.arizona.edu/>). We calculated mean annual NDVI in a 50-km radius around each study location, except for coastal and island sites, which we restricted to coastal boundaries.

We converted %FO values to proportions by dividing by 100. Trophic (i.e. dietary) diversity (D) was estimated for each study using Herrera’s trophic diversity index, given by the formula:

$$D = - \sum_{i=1}^s \log p_i$$

where p is the frequency of occurrence of the various food groups (i) (Herrera 1976). This index is appropriate for presence–absence diet data, whereas other measures such as the Shannon Index are not (Herrera 1976). D increases as more food groups are eaten and eaten less evenly relative to each other. Conversely, D decreases as fewer food groups are eaten, and eaten more evenly. We did not calculate trophic diversity for four studies that did not report FO values for arthropods ($n = 3$) and/or carrion ($n = 3$); two of those studies did not report FO values for both arthropods and carrion.

To test for bias caused by variation in sample size, study duration or sample material (scat or stomach) we constructed multivariate linear models in the package mvabund version 3.8.4 (Wang et al. 2012) within R version 3.0.2 (R Core Team 2013). We included all main terms and the interaction between sample material and sample size in the model, and used a matrix of the eight food groups (logit-transformed) as the response variable. Alpha was set at 0.05, and multivariate P -values were calculated using 1,000 residual resamples.

We used generalized additive mixed models (GAMMs) in the R package *mgcv* version 1.7-26 (Wood 2011) to model the relationship between the FO of each food group as a function of trophic diversity, latitude, longitude, mean precipitation, mean temperature and mean environmental productivity (hypotheses 1 and 2). Models were fitted using the identity link function and thin plate regression splines. Region was included as a random intercept. Significant relationships were inferred at $\alpha = 0.05$. Residuals were inspected visually and there were no problematic residual distributions for any of the models. We did not include data from Macquarie Island in analyses of latitude, longitude and mean annual temperature because the variables at those locations had extreme values that created outliers. We used GAMMs to model the consumption of each food group as a function of rabbit consumption (hypothesis 3). Additionally, to test the degree of specialization in cat diet, we fitted GAMMs using trophic diversity (D) as the predictor variable and the FO of each food group as the response variables.

Regional differences in diet composition were estimated using multivariate linear models (Wang et al. 2012). We specified models with region as the predictor variable and a matrix of the eight food groups (logit-transformed) and trophic diversity (log-transformed) as the response variables, assuming multivariate normality of errors. We made pairwise comparisons between each level of region using multivariate P -values based on 1,000 residual resamples. We then used post-hoc univariate tests with adjusted P -values to identify the individual variables that differed between regions. We plotted untransformed regional FO data for each food group to show pairwise differences between regions and we standardized trophic diversity on a scale of 0 to 1 for plotting.

Results

Cat prey

From our literature review we recorded 400 vertebrate species that feral cats feed on or kill in Australia: 123 birds (47 families), 157 reptiles (9), 58 marsupials (15), 27 rodents (1), five bats (3), 21 frogs (2) and nine medium- and large-sized exotic mammals (6; see Table B.3 in Appendix B). We found published accounts of cat predation on 28 species that are IUCN Red Listed: three critically endangered species, five endangered, eight vulnerable and 12 near threatened

(Table A.1). Cats also consumed insects from 13 orders, as well as spiders, scorpions, centipedes and crustaceans (Table B.3). Arthropods were the most commonly consumed food group across all studies (mean %FO \pm SE = 36.15 \pm 2.78), followed by rodents (28.24 \pm 3.05), birds (26.93 \pm 2.49), rabbits (25.64 \pm 3.77), reptiles (24.00 \pm 3.03), dasyurids (9.62 \pm 1.56), carrion (5.90 \pm 1.20) and medium-sized native mammals (3.84 \pm 1.29).

Sample sizes ranged from 20 to 1085 scats or stomachs with a mean of 127.7 \pm 28 SE. The multivariate linear analysis revealed no effect of origin of sample material ($F_{1,42} = 6.36$, $P = 0.578$), study duration ($F_{1,40} = 7.15$, $P = 0.499$), sample size ($F_{1,41} = 11.03$, $P = 0.242$), or the interaction between the origin of sample material and sample size ($F_{1,39} = 3.27$, $P = 0.896$) on the FO of food groups in cats' diets. We therefore pooled studies with varying sample sizes, durations and sample material for further analysis.

Table A.1 Threatened animal species consumed or killed by feral cats in Australia and their IUCN Red List status. See Table B.3 for a complete list of vertebrate species and invertebrate groups recorded as being consumed or killed by feral cats in Australia and its territorial islands.

Critically endangered	Near threatened
<i>Bettongia penicillata</i>	<i>Antechinus godmani</i>
<i>Burramys parvus</i>	<i>Bettongia lesueur</i>
<i>Emoia nativitatis</i>	<i>Dasyurus geoffroii</i>
	<i>Ducula whartoni</i>
Endangered	<i>Mastacomys fuscus</i>
<i>Dasyurus hallucatus</i>	<i>Perameles gunnii</i>
<i>Lagostrophus fasciatus</i>	<i>Petrogale lateralis</i>
<i>Myrmecobius fasciatus</i>	<i>Petrogale penicillata</i>
<i>Onychogalea fraenata</i>	<i>Petrogale xanthopus</i>
<i>Perameles bougainville</i>	<i>Petroica phoenicea</i>
	<i>Phascogale tapoatafa</i>
Vulnerable	<i>Sminthopsis douglasi</i>
<i>Gallirallus australis*</i>	
<i>Eudyptes chrysocome</i>	
<i>Lagorchestes hirsutus</i>	
<i>Leipoa ocellata</i>	
<i>Macrotis lagotis</i>	
<i>Pteropus melanotus</i>	
<i>Setonix brachyurus</i>	
<i>Uromys hadrourus</i>	
*This species is endemic to New Zealand, but was deliberately introduced to Macquarie Island where it was predated by cats. Both have since been eradicated from the island.	

Biogeographical patterns

Fourteen GAMMs yielded significant relationships between cat food groups and predictor variables (Table A.2, Figure A.2). The consumption of arthropods and rabbits showed quadratic relationships with latitude, with consumption highest at mid-latitudes (25 to 35°S) and least to the north and south of the continent (Figure A.2a,b, Table A.2). Rodent consumption averaged approximately 25% FO at the highest latitudes and increased sharply, north of 25°S (Figure A.2c). The pattern of reptile consumption was more complex, showing a bi-modal relationship with latitude, peaking at 22°S and 29°S with a trough at 25°S (Figure A.2d). The consumption of medium-sized mammals showed a weak positive relationship with longitude (Figure A.2e, Table A.2). The frequency of reptiles in cats' diets increased with mean annual temperature, whereas rodent FO increased above 20°C mean annual temperature (Figure A.2f,g) and rabbit FO showed a quadratic relationship with temperature, being highest at 15–22°C (Figure A.2h). Arthropod and reptile FOs decreased with greater mean annual precipitation, and medium-sized mammal FO had a weak positive relationship with precipitation (Figure A.2i–k, Table A.2). Reptile and arthropod FOs decreased with greater environmental productivity, whereas that for medium-sized mammals increased (Figure A.2l–n). No other combinations of environmental variables and food groups had statistically significant relationships (Table A.2).

Table A.2 Generalized additive mixed modelling (GAMM) results for the relationship between environmental and geographical variables, food groups (FO) and trophic (dietary) diversity (D) of feral cats in Australia.

		Latitude	Longitude	Annual precipitation	Annual temperature	NDVI	Trophic diversity
Arthropods	e.d.f. =	3.19	1.00	1.00	2.38	2.04	1.00
	$F =$	4.08	1.62	12.56	2.14	6.11	6.81
	$P =$	0.007**	0.209	< 0.001***	0.109	0.003**	0.012*
	adj- $R^2 =$	0.261	0.014	0.204	0.108	0.239	0.117
Reptiles	e.d.f. =	7.36	1.84	1.00	1.20	3.42	1.26
	$F =$	4.64	1.31	8.66	14.44	3.35	4.83
	$P =$	< 0.001***	0.278	0.005**	< 0.001***	0.016*	0.022*
	adj- $R^2 =$	0.432	0.049	0.138	0.300	0.209	0.110
Birds	e.d.f. =	1.00	1.57	1.00	1.00	1.00	1.25
	$F =$	1.21	1.67	1.88	3.49	1.61	2.51
	$P =$	0.276	0.198	0.177	0.068	0.211	0.104
	adj- $R^2 =$	0.005	0.040	0.018	0.049	0.012	0.075
Rabbits	e.d.f. =	2.44	1.00	5.18	3.33	3.35	1.50
	$F =$	3.81	0.49	1.84	4.11	1.88	1.37
	$P =$	0.016*	0.490	0.112	0.006**	0.129	0.259
	adj- $R^2 =$	0.191	-0.011	0.154	0.245	0.117	0.027
Rodents	e.d.f. =	2.01	1.68	1.00	3.15	1.00	1.00
	$F =$	3.08	2.84	0.142	3.22	0.05	9.02
	$P =$	0.044*	0.067	0.708	0.022*	0.822	0.004**
	adj- $R^2 =$	0.128	0.100	-0.018	0.198	-0.020	0.154
Dasyurids	e.d.f. =	1.00	1.00	6.43	1.00	3.20	1.00
	$F =$	2.66	0.27	1.27	3.99	1.58	0.90
	$P =$	0.110	0.604	0.286	0.052	0.196	0.348
	adj- $R^2 =$	0.035	-0.016	0.101	0.059	0.102	-0.002
Medium-sized mammals	e.d.f. =	1.78	2.27	1.58	1.72	2.03	1.00
	$F =$	2.48	3.57	4.80	0.99	6.12	0.107
	$P =$	0.089	0.024*	0.013*	0.380	0.003**	0.745
	adj- $R^2 =$	0.100	0.155	0.141	0.031	0.243	-0.021
Carrion	e.d.f. =	1.00	1.00	3.38	1.00	1.83	4.28
	$F =$	0.43	0.69	1.65	0.08	1.05	1.12
	$P =$	0.514	0.41	0.177	0.783	0.360	0.367
	adj- $R^2 =$	-0.013	-0.007	0.114	-0.021	0.034	0.076
Trophic diversity	e.d.f. =	1.00	1.89	1.00	5.89	1.00	-
	$F =$	2.98	2.33	1.88	2.31	3.70	-
	$P =$	0.091	0.101	0.178	0.046*	0.061	-
	adj- $R^2 =$	0.043	0.095	0.020	0.225	0.058	-

e.d.f., estimated degrees of freedom.
NDVI, normalized difference vegetation index.
* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

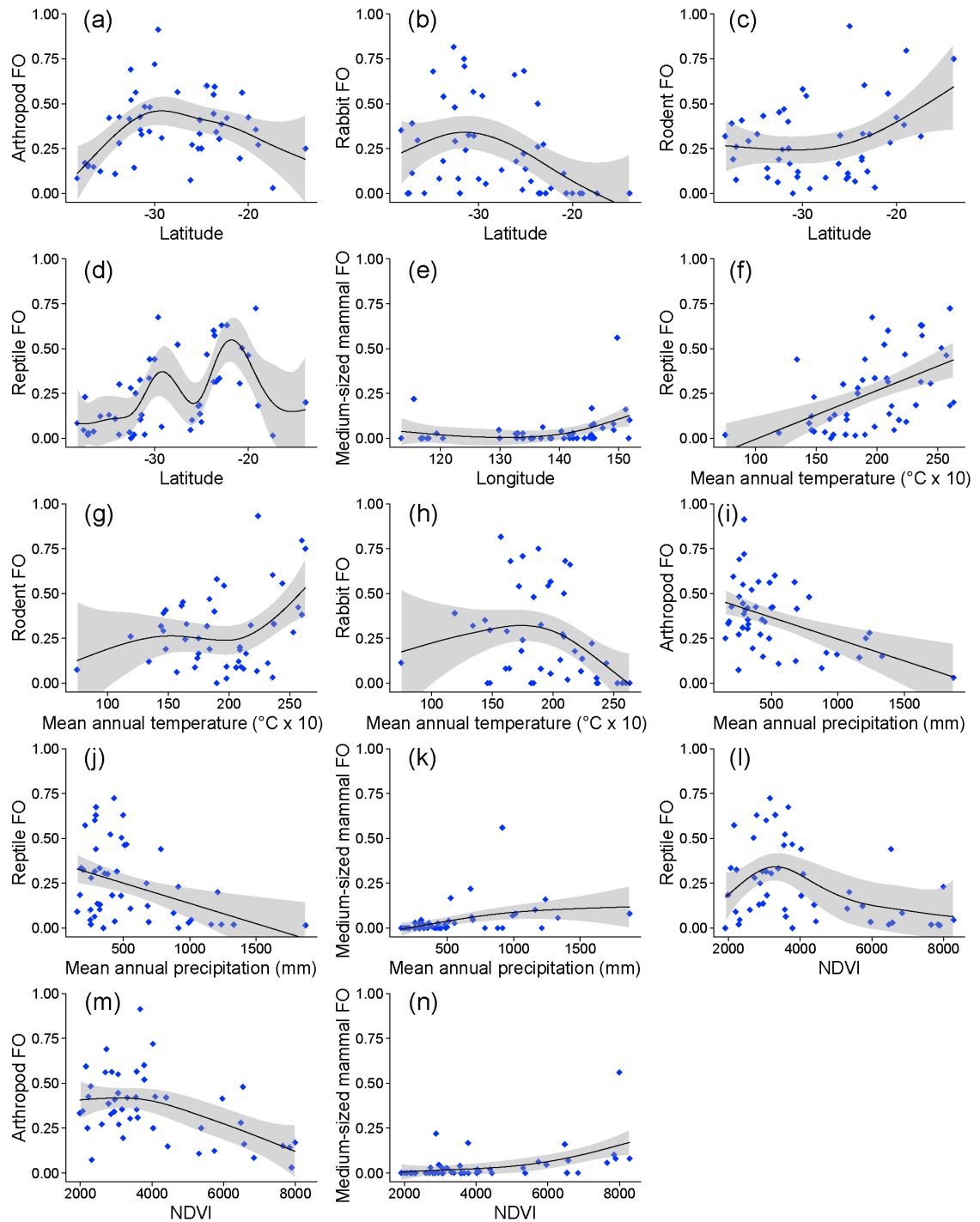


Figure A.2 The frequency of occurrence (FO) of feral cat food groups in Australia modelled as a function of environmental and geographical predictors: (a–d) latitude with arthropod, rabbit, rodent and reptile FOs; (e) longitude with medium-sized mammal FO; (f–h) mean annual temperature ($^{\circ}\text{C} \times 10$) with reptile, rodent and rabbit FOs; (i–k) mean annual precipitation (mm) with arthropod, reptile and medium-sized mammal FOs; and (l–n) environmental productivity (NDVI) with reptile, arthropod and medium-sized mammal FOs. The solid black line is the fitted model mean and the shaded area represents the 95% confidence intervals of the predicted mean.

Dietary composition varied across regions ($F_{5,39} = 21.90, P = 0.002$) and pairwise tests showed that the ISL, TROP and SE regions were all significantly different from each other and all other regions, except for the SE/EAST pair (Table A.3). The other pairs that did not differ from each other were all combinations of ARID, EAST and SW (Table A.3). Univariate tests showed that consumption of medium-sized mammals in the SE region was higher than in all others ($F = 4.75, P = 0.002$; Figure A.3a) and rabbits were not consumed in the TROP region, except for a small number in one study ($F = 4.07, P = 0.006$; Figure A.3a). The mean FO of arthropods ($F = 1.09, P = 0.385$), reptiles ($F = 2.03, P = 0.10$), birds ($F = 1.75, P = 0.144$), rodents ($F = 1.52, P = 0.203$), dasyurids ($F = 2.51, P = 0.051$) and carrion ($F = 2.20, P = 0.073$) displayed no statistically significant patterns across regions (Figure A.3a,b); although consumption of reptiles was lowest on islands and in the SE region, that of birds was highest on islands, and dasyurids were not consumed on islands (Figure A.3a,b).

Table A.3 Pairwise regional differences in feral cat diet composition in Australia (FO, logit-transformed; and trophic diversity, log-transformed) based on multivariate linear models.

		ARID	EAST	ISL	SE	SW
EAST	$F =$ $P =$	8.19 0.507	-	-	-	-
ISL	$F =$ $P =$	23.84 0.041*	21.25 0.046*	-	-	-
SE	$F =$ $P =$	34.50 < 0.001***	15.27 0.133	26.93 0.017*	-	-
SW	$F =$ $P =$	5.28 0.755	8.64 0.457	27.67 0.015*	23.66 0.030*	-
TROP	$F =$ $P =$	22.65 0.032*	32.60 0.004**	26.68 0.028*	41.05 < 0.001***	22.67 0.046*

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

ARID, deserts and xeric shrublands; EAST, eastern inland shrub/grass/woodlands and savannas; ISL, islands; SE, south-east temperate forests and heath; SW, south-west shrublands, woodlands and forests; TROP, tropical grasslands, savannas, shrublands and forests.

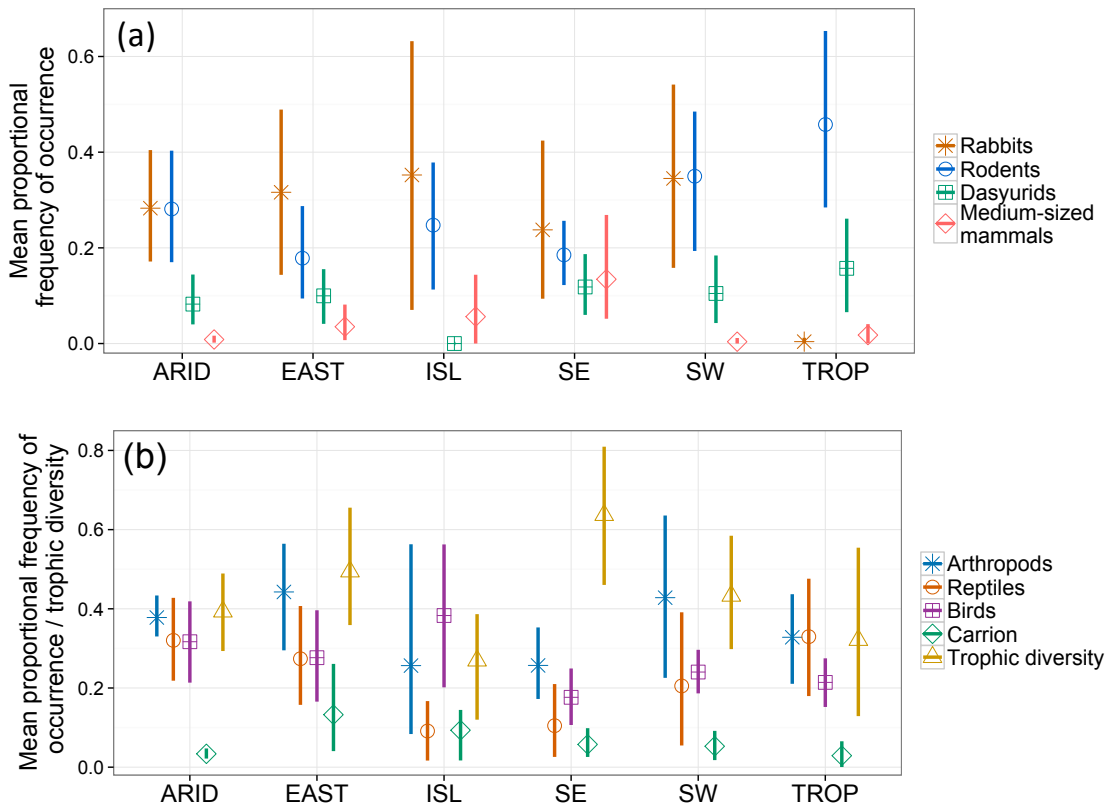


Figure A.3 Mean regional frequency of occurrence for (a) rabbits, rodents, dasyurids and medium-sized mammals and (b) arthropods, reptiles, birds, carrion and trophic diversity of feral cats in Australia. Trophic diversity has been standardized on a scale of 0 to 1. Error bars are bootstrapped 95% confidence intervals. ARID, deserts and xeric shrublands; EAST, eastern inland shrub/grass/woodlands and savannas; ISL, islands; SE, south-east temperate forests and heath; SW, south-west shrublands, woodlands and forests; TROP, tropical grasslands, savannas, shrublands and forests.

Trophic diversity and the influence of rabbits

The univariate test of trophic diversity from the multivariate linear model did not show a statistical relationship across regions ($F = 1.98, P = 0.101$), although inspection of Figure A.3b shows that mean trophic diversity on islands tended to be lower than in all other regions. Trophic diversity also tended to decrease with greater mean annual temperature (Figure A.4d) and higher trophic diversity was associated with lower frequencies of arthropods, rodents and reptiles in cats' diets (Figure A.4a–c, Table A.2). The consumption of rabbits was negatively correlated with consumption of rodents (estimated degrees of freedom, e.d.f. = 1.00, $F = 5.65, P = 0.022, \text{adj-}R^2 = 0.088$; Figure A.4e) and dasyurids (e.d.f. = 1.44, $F = 5.26, P = 0.012, \text{adj-}R^2 = 0.129$; Figure A.4f). Consumption of rabbits did not show any relationship with consumption of arthropods (e.d.f. = 1.00, $F = 1.29, P = 0.262, \text{adj-}$

$R^2 = 0.006$), reptiles (e.d.f. = 3.11, $F = 1.75$, $P = 0.156$, adj- $R^2 = 0.103$), birds (e.d.f. = 1.00, $F = 2.45$, $P = 0.124$, adj- $R^2 = 0.029$), medium-sized mammals (e.d.f. = 1.17, $F = 2.84$, $P = 0.085$, adj- $R^2 = 0.047$) or carrion (e.d.f. = 2.50, $F = 0.66$, $P = 0.588$, adj- $R^2 = 0.012$).

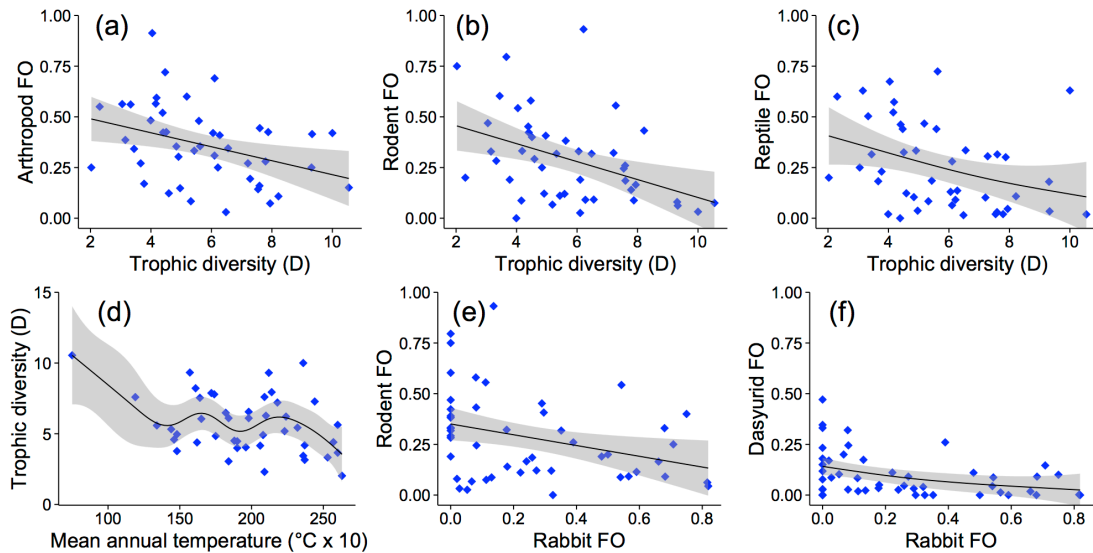


Figure A.4 Generalized additive mixed model relationships for: (a–c) trophic diversity of feral cats in Australia and frequency of occurrence (FO) of arthropods, rodents and reptiles; (d) trophic diversity and mean annual temperature ($^{\circ}\text{C} \times 10$); and (e–f) rabbit FO with rodent and dasyurid FOs. The solid black line is the fitted model mean and the shaded area represents the 95% confidence intervals of the predicted mean.

Discussion

Biogeographical patterns

Is reptile consumption greatest in arid areas?

The data support our first hypothesis: consumption of reptiles by feral cats is negatively correlated with rainfall, and is more frequent in arid regions. The importance of reptiles in the diet of cats in these areas is probably related to the high reptile species richness in these regions. Lizard species richness is highest in the central deserts and tropical north-east and -west, and decreases with greater actual evapotranspiration (Schall & Pianka 1978; Powney et al. 2010)—parameters which closely parallel those for which we recorded the highest reptile consumption by cats. Also, the SE region recorded the lowest mean consumption of reptiles and corresponds to the area of lowest lizard species richness in Australia

(Powney et al. 2010). Previous studies from outside Australia have also related patterns of reptile consumption by cats to biogeographic trends in reptile species richness (Fitzgerald & Turner 2000; Lozano et al. 2006; Bonnaud et al. 2011), but the prevalence of reptiles in cats' diets in Australia is higher than on many other continents, probably because of the higher species richness (and abundance) of reptiles in Australia, especially in arid areas (Schall & Pianka 1978). For instance, Fitzgerald and Turner (2000) found that reptiles comprised only 1.6% mean FO of feral cat diet in northern hemisphere continental studies, compared with 32.7% for Australia (23.6% in this study).

Does reptile and arthropod consumption decrease with increasing latitude?

Although feral cats consumed reptiles and arthropods less frequently at higher latitudes (i.e. southern Australia), the consumption of these two groups peaked at the mid-latitudes of the continent. These patterns do not support our prediction and are in contrast to the latitudinal patterns recorded in previous studies elsewhere in the world (Pearre & Maass 1998; Lozano et al. 2006; Díaz-Ruiz et al. 2011; Bonnaud et al. 2012). The high reptile species richness of Australia's mid-latitude arid centre (Schall & Pianka 1978; Powney et al. 2010) may explain why reptiles were consumed most frequently at mid-, rather than low latitudes. The bi-modal relationship between reptile consumption and latitude probably relates to the fluctuating nature of prey availability in this arid region. Arid Australia experiences pulses of environmental productivity following periods of above-average rainfall that drive population explosions of small mammals (Letnic & Dickman 2010). Reptiles are less likely to be consumed by cats when small mammals are at high densities during such pulses (Pavey et al. 2008; Spencer et al. 2014b), so environmentally driven shifts in the abundances of small mammals may explain the fluctuating relationship observed in the mid-latitude band.

Although continental-scale information on the biogeography of Australian arthropods is scarce, the atypical latitudinal pattern in arthropod consumption recorded here may be related to the importance of this group to the diet of cats living in arid and semi-arid regions. Arthropods are small compared to other prey and consist mostly of indigestible exoskeleton, hence they provide cats with little energy per unit consumed and are not their preferred food source (Fitzgerald &

Turner 2000). Increased consumption of arthropods by feral cats in harsher environmental conditions (i.e. regions with lower rainfall and productivity) suggests that cats will switch to this prey when their preferred prey are less numerous and they are food stressed (Catling 1988).

Is there an inverse relationship between consumption of rabbits and small rodents and dasyurids?

Rabbits are often the staple prey of feral cats in Australia; however, as predicted by our third hypothesis, we found that where rabbits occur in cats' diets less frequently, the frequency of small dasyurids and rodents in cats' diets increases. Studies from Europe also found that where the wildcat and red fox *Vulpes vulpes* consumed fewer rabbits, they consumed more small mammals (Malo et al. 1999; Lozano et al. 2006; Díaz-Ruiz et al. 2011). Feral cats, like other carnivores, are able to switch between alternative food sources when their preferred prey decreases in availability—referred to as 'prey-switching' (Liberg 1984; Catling 1988). Like the wildcat in Eurasia (Lozano et al. 2006), the feral cat in Australia uses a facultative feeding strategy, feeding mainly on rabbits when they are available, but switching to small mammals if rabbits decrease in availability or are unavailable altogether. For example, in this study the highest frequencies of rodent and dasyurid in the diet of cats occurred in the TROP region where rabbits are generally not available for cats to feed on due to environmental constraints on their survival (Williams et al. 1995; West 2008).

Medium-sized mammals

Consumption of medium-sized native mammals, mostly possums (*Trichosurus* and *Pseudocheirus* spp.) and bandicoots (*Isodon* and *Perameles* spp.), was greatest in the south-east of the continent. The high FO for this group in the SE region may be related to their availability. Twenty-nine small- and medium-sized mammals have become extinct in Australia in just over 200 years (Woinarski et al. 2014) and this pattern has been strongest in the low rainfall, inland parts of the continent (McKenzie et al. 2007). In comparison, the SE region retains a mostly complete mammal fauna (McKenzie et al. 2007), and proportionally more medium-sized arboreal mammals occur in high compared to low rainfall areas in Australia (Johnson & Isaac 2009). Interestingly though, consumption of medium-sized mammals was low in the TROP region, even though mammal extinction rates have

also been low in northern Australia (McKenzie et al. 2007). Some mammals, however, have shown sharp declines in parts of this region since around the early 1990s (Braithwaite & Muller 1997; Woinarski et al. 2001; Woinarski et al. 2010), so it is difficult to corroborate the patterns observed here with changes in the extent and size of native mammal populations. Additional data on cat diet and prey availability from elsewhere in this region should help clarify why medium-sized mammals were not heavily depredated in the TROP region studies reviewed here.

Conservation implications

Our most significant finding was a continental-scale pattern of prey-switching from rabbits to small mammals, which has previously been recorded only at the local scale (Catling 1988). This has important implications for conservation managers, since control programmes aimed at culling rabbits could potentially decrease the availability of a preferred food source for cats and then lead to greater predation of native mammals (Courchamp et al. 1999; Norbury 2001; Murphy et al. 2004). The interplay between cat diet and prey species diversity and abundance at a continental scale is complex and thus requires conservation managers to investigate these interactions further at a local landscape level.

Our findings support previous research in suggesting that the feral cat is an opportunistic, generalist carnivore capable of exploiting a diverse range of vertebrate and invertebrate prey across Australia, including lizards, snakes, frogs, marine and terrestrial bird species, arboreal and ground-dwelling marsupials, rodents, rabbits and arthropods. We recorded 400 vertebrate species that cats consume or kill, which is more than double the 179 vertebrate prey species recorded on 40 islands worldwide (Bonnaud et al. 2011). Feral cats in Australia and its territorial islands depredate 16 globally threatened mammals, birds and reptiles, and 12 other 'near-threatened' species. Our prey list includes only those species that have been detected in dietary or predation studies, so it is likely that there are additional threatened species that were not detected in the studies included here, but are still depredated by feral cats.

We did, however, find records of cat predation on numerous 'critical weight range' mammal species—a group that has suffered severe range declines and

extinctions over the past 200 years (Johnson 2006; Woinarski et al. 2014). Predation by feral cats is a primary factor contributing to these declines and is recognised as an ongoing threat to biodiversity in Australia, especially in the north (Woinarski et al. 2011; Woinarski et al. 2014). Secure populations of threatened mammals have been established on predator-free islands and fenced mainland reserves (Burbidge 1999; Long & Robley 2004); however, fencing is expensive and requires ongoing maintenance, and is thus limited in scale as a conservation option. Broad-scale control of cats using poison baiting can reduce cat population densities in some areas (Algar et al. 2007; Christensen et al. 2013; Algar et al. 2013), but cats can still exterminate threatened mammal populations even when subjected to intensive lethal control (Christensen & Burrows 1994; Gibson et al. 1994). Reducing the impact of feral cats on Australian mammals remains a formidable challenge for conservation managers.

The persistence of cats on islands that lack the larger-bodied mammal prey found on the mainland is often aided by seabirds that nest in dense colonies on the ground, which provide cats with a reliable food resource, at least seasonally (Fitzgerald & Turner 2000; Bonnaud et al. 2011); although introduced rabbits are also eaten when available. Feral cats endanger seabird breeding colonies on islands across the globe, and the removal of cats can trigger population recoveries (Ratcliffe et al. 2010; Bonnaud et al. 2012; Hervías et al. 2012). We found that seabirds form a large component of cats' diets on Australian islands (Jones 1977; Copley 1991; Hayde 1992; Beh 1995; Kirkwood et al. 2013), so population reduction or eradication of cats is needed to protect these colonies (Twyford et al. 2000; Robinson & Copson 2014).

As a consequence of our study, we recommend that future research should: (1) investigate the dietary response of cats to fluctuating climatic conditions and prey availability; (2) focus on north-western and far north-eastern parts of tropical Australia; (3) target a greater range of islands, including Tasmania; (4) attempt to cover all seasons of cats' activity; and (5) endeavour to record the relative contribution by mass or volume of different food groups to cats' diets.

Acknowledgements

We thank the many researchers whose published work was examined in this study. T.S.D. was supported by research funding and scholarships from Edith Cowan University, Earthwatch Institute Australia and the Holsworth Wildlife Research Endowment while conducting this research. Bush Heritage Australia provided access to their property (Charles Darwin Reserve) for sample collection and Georgeanna Story conducted the dietary analysis of those samples. Funding for C.R.D. was provided by the Australian Research Council. G.E. acknowledges Rachel Paltridge, Nicki de Preu and David Gibson for their contribution towards the unpublished data sets from the Northern Territory. P.M. thanks the Kangaroo Island community for assisting with sample collection. S.R. acknowledges Geoff Copson and the many Tasmanian Parks and Wildlife Service Macquarie Island staff for their contribution towards the unpublished data set from Macquarie Island.

Supplementary materials

Supplementary materials can be found in Appendix B:

Table B.1 Bibliography of feral cat diet studies from Australia.

Table B.2 Summary information for data sets used in the analyses.

Table B.3 List of feral cat prey species from Australia.

Appendix B.

Supplementary materials for Appendix A

Table B.1 Bibliography of published studies that contain data on the diet of feral cats *Felis catus* in Australia. Bold text indicates a study that was included in our analyses.

Amansyah, S. (1997) *Ecology of feral cats, Felis catus L., in an urban parkland environment.* Master's thesis, Macquarie University, Sydney.

Barratt, D.G. (1997) Predation by house cats, *Felis catus* (L.), in Canberra, Australia. I. Prey composition and preference. *Wildlife Research*, 24, 263–277.

Bayly, C.P. (1978) A comparison of the diets of the red fox and the feral cat in an arid environment. *South Australian Naturalist*, 53, 20–28.

Beh, C.L. (1995) The winter ecology of the feral cat, *Felis catus* (Linnaeus 1758), at Wedge Island, Tasmania. Honours Thesis, University of Tasmania, Hobart.

Brunner, H. & Wallis, R. (1986) Roles of predator scat analysis in Australian mammal research. *Victorian Naturalist*, 103, 79–87.

Brunner, H., Moro, D., Wallis, R. & Andrasek, A. (1991) Comparison of the diets of foxes, dogs and cats in an urban park. *Victorian Naturalist*, 108, 34–37.

Buckmaster, A.J. (2011) *Ecology of the feral cat (Felis catus) in the tall forests of Far East Gippsland.* PhD thesis, University of Sydney, Sydney.

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Table B.2 Summary of the data sets used in analyses, with first author of publication or author of unpublished data set. Refer to Table B.1 for full references.

First author	Location ^A	Year published	Region ^B	Sample size (scats/ stomachs)	Study duration (months)	Latitude	Longitude
Algar	Mid-west mine sites, WA	unpublished	ARID	118	136	-26.00	120.40
Algar	Karara station, WA	unpublished	SW	24	24	-29.24	116.70
Amansyah	Lane Cove National Park, NSW	1997	SE	51	15	-33.79	151.16
Buckmaster	Gippsland, VIC	2009	SE	22	20	-37.57	149.15
Burnett	Wet Tropics World Heritage Area, QLD	2001	TROP	123	60	-17.38	145.82
Catling	Yathong Nature Reserve, NSW	1988	EAST	112	25	-33.75	145.50
Coman	'Primary habitat', VIC	1972	SE	53	24	-37.10	147.30
Coman	'Secondary habitat', VIC	1972	EAST	27	24	-36.50	143.00
Dickman	'Plains country', QLD	unpublished	TROP	26	12	-20.00	140.33
Dickman	Rottneest Island, WA	unpublished	ISL	32	29	-32.00	115.50
Dickman	Wheatbelt, WA	unpublished	SW	48	20	-31.51	117.75
Doherty	Charles Darwin Reserve, WA	unpublished	SW	45	13	-29.61	117.00
Edwards ^C	Burt Plain, NT	unpublished	ARID	33	39	-23.10	133.80
Edwards ^C	Mitchell Grass Downs, NT	unpublished	TROP	181	49	-18.95	135.19
Edwards ^C	Tanami, NT	unpublished	ARID	36	68	-20.91	133.00
Edwards ^C	Top End, NT	unpublished	TROP	20	68	-13.91	132.84
Edwards ^C	Alice Springs (MAC/FIN bioregions), NT	unpublished	ARID	108	84	-23.70	133.88
Foulkes	Irving Creek, NT	2001	ARID	22	32	-25.16	129.82
Glen	Barrington Tops, NSW	2010	SE	49	26	-32.17	151.83
Holden	Flinders Ranges National Park, SA	2002	ARID	288	60	-31.38	138.60
Jones	Mallee National Park, VIC	1981	EAST	131	36	-34.85	141.62
Jones	Kincheha National Park, NSW	1981	EAST	65	36	-32.54	142.29
Jones	Eastern Highlands, VIC	1981	SE	117	36	-37.09	145.41
Jones	Macquarie Island	1977	ISL	756	15	-54.62	158.86
Kirkwood	Phillip Island, VIC	2013	ISL	239	144	-38.25	145.50
Kutt	North-central QLD	2010	TROP	169	24	-22.30	145.08
Lapidge	South-west QLD	2001	EAST	49	33	-25.33	145.40
Mahood	Gnalta National Park, NSW	1980	ARID	79	-	-31.05	142.33
Mahon	Simpson Desert, QLD	1999	ARID	377	84	-23.60	138.48

First author	Location ^A	Year published	Region ^B	Sample size (scats/stomachs)	Study duration (months)	Latitude	Longitude
Martin	Wheatbelt, WA	1996	SW	31	47	-32.50	118.00
Martin	Pastoral, WA	1996	SW	50	47	-30.00	118.00
Masters	Kangaroo Island, SA	unpublished	ISL	65	84	-35.78	137.21
Misfud	Julia Creek, QLD	2012	TROP	187	36	-20.66	141.75
Molsher	Lake Burrendong, NSW	1999	SE	499	36	-32.67	149.17
O'Connell	Fitzgerald River National Park, WA	2010	SW	41	60	-34.20	119.37
Palmer	Mulyungarie Station, SA	unpublished	ARID	40	36	-31.55	140.79
Palmer	Cunnamulla, QLD	unpublished	EAST	23	132	-27.55	145.91
Palmer	Blackall, QLD	unpublished	EAST	30	24	-24.90	145.00
Palmer	Muncoonie Lakes, QLD	unpublished	ARID	27	23	-25.20	138.68
Paltridge	Tennant, NT	2002	ARID	76	27	-19.20	132.67
Paltridge	Kintore, NT	2002	ARID	70	20	-22.85	129.95
Pavey	Simpson Desert, NT	2008	ARID	44	27	-25.00	135.60
Read	Roxby Downs, SA	2001	ARID	316	121	-30.56	136.90
Risbey	Heirisson Prong, WA	1999	SW	109	57	-26.17	113.38
Robinson	Macquarie Island	unpublished	ISL	1085	312	-54.62	158.86
Strong	Southern NT	1983	ARID	20	36	-23.70	133.88
Triggs	Croajingalong National Park, VIC	1984	SE	48	20	-37.42	149.75
van Herk	Armidale, NSW	1980	SE	25	36	-30.51	151.67
Yip	Longreach, QLD	2013	TROP	73	24	-23.43	144.25

^A NSW, New South Wales; NT, Northern Territory; QLD, Queensland; SA, South Australia; VIC, Victoria; WA, Western Australia.

^B ARID, deserts and xeric shrublands; EAST, eastern inland shrub/grass/woodlands and savannas; ISL, islands; SE, south-east temperate forests and heath; SW, south-west shrublands, woodlands and forests; TROP, tropical grasslands, savannas, shrublands and forests.

^C A subset of Edwards' unpublished data is used in a study that we did not include in our analyses: Paltridge, R., Gibson, D., & Edwards, G. (1997) Diet of the feral cat (*Felis catus*) in central Australia. *Wildlife Research*, **24**, 67–76.

Table B.3 List of vertebrate species and invertebrate groups recorded as being consumed or killed by feral cats in Australia and its territorial islands and their IUCN Red List Conservation status. * introduced species; ^ cat predation inferred as cause of mortality; CR, critically endangered; EN, endangered; VU, vulnerable; NT, near threatened; DD, data deficient (IUCN, 2013); *** the European rabbit (*Oryctolagus cuniculus*) is classed as 'near threatened' in its native range, but is an introduced pest in Australia.

	Family	Species	IUCN status
Mammals			
Marsupialia	Acrobatidae	<i>Acrobates pygmaeus</i>	
	Burramyidae	<i>Burramys parvus</i>	CR
		<i>Cercartetus caudatus</i>	
	Dasyuridae	<i>Antechinomys laniger</i>	
		<i>Antechinus adustus</i>	
		<i>Antechinus flavipes</i>	
		<i>Antechinus godmani</i>	NT
		<i>Antechinus stuartii</i>	
		<i>Antechinus swainsonii</i>	
		<i>Dasyercus cristicauda</i>	
		<i>Dasykaluta rosamondae</i>	
		<i>Dasyurus geoffroii</i>	NT
		<i>Dasyurus hallucatus</i>	EN
		<i>Ningau ridei</i>	
		<i>Ningau timealeyi</i>	
		<i>Phascogale tapoatafa</i>	NT
		<i>Planigale ingrami</i>	
		<i>Planigale maculata</i>	
		<i>Planigale tenuirostris</i>	
		<i>Sminthopsis crassicaudata</i>	
		<i>Sminthopsis dolichura</i>	
		<i>Sminthopsis douglasi</i>	NT
		<i>Sminthopsis gilberti</i>	
		<i>Sminthopsis hirtipes</i>	
		<i>Sminthopsis macroura</i>	
		<i>Sminthopsis ooldea</i>	
		<i>Sminthopsis youngsoni</i>	
	Macropodidae	<i>Lagorchestes hirsutus</i>	VU
		<i>Lagostrophus fasciatus</i>	EN
		<i>Macropus fuliginosus</i>	
		<i>Macropus giganteus</i>	
		<i>Macropus robustus</i>	
		<i>Macropus rufus</i>	
		<i>Onychogalea fraenata</i>	EN
		<i>Petrogale lateralis</i>	NT
		<i>Petrogale penicillata</i> ^	NT
		<i>Petrogale xanthopus</i>	NT
		<i>Setonix brachyurus</i>	VU
		<i>Thylogale</i> sp.	
		<i>Wallabia bicolor</i>	
	Myrmecobiidae	<i>Myrmecobius fasciatus</i>	EN
	Notoryctidae	<i>Notoryctes typhlops</i>	DD
	Peramelidae	<i>Isoodon macrourus</i>	
		<i>Isoodon obesulus</i>	
		<i>Perameles bougainville</i> ^	EN
		<i>Perameles gunnii</i>	NT
		<i>Perameles nasuta</i>	
	Petauridae	<i>Petaurus breviceps</i>	
	Phalangeridae	<i>Trichosurus vulpecula</i>	
	Potoroidae	<i>Bettongia lesueur</i>	NT

		<i>Bettongia penicillata</i>	CR
	Pseudocheiridae	<i>Petauroides volans</i>	
		<i>Pseudocheirus peregrinus</i>	
		<i>Pseudochirulus herbertensis</i>	
	Tachyglossidae	<i>Tachyglossus aculeatus</i>	
	Tarsipedidae	<i>Tarsipes rostratus</i>	
	Thylacomyidae	<i>Macrotis lagotis</i>	VU
	Vombatidae	<i>Vombatus ursinus</i>	
Chiroptera	Molossidae	<i>Mormopterus planiceps</i>	
	Pteropodidae	<i>Pteropus melanotus</i>	VU
	Vespertilionidae	<i>Chalinolobus gouldii</i>	
		<i>Nyctophilus geoffroyi</i>	
		<i>Vespadelus vulturinus</i>	
Eutheria	Muridae	<i>Hydromys chrysogaster</i>	
		<i>Leggadina forresti</i>	
		<i>Leggadina lakedownensis</i>	
		<i>Mastacomys fuscus</i>	NT
		<i>Melomys burtoni</i>	
		<i>Melomys cervinipes</i>	
		<i>Mus musculus*</i>	
		<i>Notomys alexis</i>	
		<i>Notomys mitchellii</i>	
		<i>Pogonomys mollipilosus</i>	
		<i>Pseudomys albocinereus</i>	
		<i>Pseudomys bolami</i>	
		<i>Pseudomys delicatulus</i>	
		<i>Pseudomys desertor</i>	
		<i>Pseudomys hermannsburgensis</i>	
		<i>Pseudomys nanus</i>	
		<i>Rattus colletti</i>	
		<i>Rattus fuscipes</i>	
		<i>Rattus leucopus</i>	
		<i>Rattus lutreolus</i>	
		<i>Rattus norvegicus</i>	
		<i>Rattus rattus*</i>	
		<i>Rattus tunneyi</i>	
		<i>Rattus villosissimus</i>	
		<i>Uromys caudimaculatus</i>	
		<i>Uromys hadrourus</i>	VU
		<i>Zyzomys argurus</i>	
Eutheria	Introduced	<i>Bos taurus*</i>	
		<i>Camelus dromedaries*</i>	
		<i>Canis lupus*</i>	
		<i>Capra hircus*</i>	
		<i>Felis catus*</i>	
		<i>Lepus europaeus*</i>	
		<i>Oryctolagus cuniculus*</i>	NT***
		<i>Ovis aries*</i>	
		<i>Sus scrofa*</i>	
Reptiles Squamata	Agamidae	<i>Amphibolurus burnsi</i>	
		<i>Amphibolurus gilberti</i>	
		<i>Amphibolurus muricatus</i>	
		<i>Amphibolurus temporalis</i>	
		<i>Ctenophorus fordi</i>	
		<i>Ctenophorus nuchalis</i>	
		<i>Ctenophorus pictus</i>	
		<i>Ctenophorus reticulatus</i>	
		<i>Moloch horridus</i>	
		<i>Pogona barbata</i>	
		<i>Pogona minor</i>	
		<i>Pogona nullabor</i>	
		<i>Pogona vitticeps</i>	

	<i>Tympanocryptis intima</i>
	<i>Tympanocryptis lineata</i>
	<i>Tympanocryptis tetraporophora</i>
Elapidae	<i>Brachyuropis australis</i>
	<i>Brachyuropis fasciolatus</i>
	<i>Brachyuropis incinctus</i>
	<i>Brachyuropis semifasciatus</i>
	<i>Cryptophis boschmai</i>
	<i>Demansia olivacea</i>
	<i>Demansia psammophis</i>
	<i>Denisonia devisi</i>
	<i>Drysdalia coronoides</i>
	<i>Furina diadema</i>
	<i>Furina ornata</i>
	<i>Hoplocephalus bitorquatus</i>
	<i>Notechis scutatus</i>
	<i>Parasuta spectabilis</i>
	<i>Pseudechis australis</i>
	<i>Pseudonaja affinis</i>
	<i>Pseudonaja ingrami</i>
	<i>Pseudonaja modesta</i>
	<i>Pseudonaja textilis</i>
	<i>Simoselaps anomalus</i>
	<i>Simoselaps bertholdi</i>
	<i>Suta punctata</i>
	<i>Suta suta</i>
	<i>Vermicella snelli</i>
Gekkonidae	<i>Amalosia rhombifer</i>
	<i>Christinus marmoratus</i>
	<i>Cyrtodactylus</i> sp.
	<i>Diplodactylus conspicillatus</i>
	<i>Diplodactylus granariensis</i>
	<i>Diplodactylus pulcher</i>
	<i>Diplodactylus tessellatus</i>
	<i>Diplodactylus vittatus</i>
	<i>Gehyra australis</i>
	<i>Gehyra catenata</i>
	<i>Gehyra nana</i>
	<i>Gehyra variegata</i>
	<i>Hemidactylus frenatus</i>
	<i>Heteronotia binoei</i>
	<i>Heteronotia spelea</i>
	<i>Lucasium byrnei</i>
	<i>Lucasium damaeum</i>
	<i>Lucasium steindachneri</i>
	<i>Lucasium stenodactylum</i>
	<i>Nephrurus asper</i>
	<i>Nephrurus levis</i>
	<i>Oedura marmorata</i>
	<i>Rhynchoedura ornata</i>
	<i>Strophurus ciliaris</i>
	<i>Strophurus intermedius</i>
	<i>Strophurus spinigerus</i>
	<i>Underwoodisaurus milii</i>
Pygopodidae	<i>Aprasia inaurita</i>
	<i>Delma nasuta</i>
	<i>Delma tinctoria</i>
	<i>Lialis burtonis</i>
	<i>Pygopus nigriceps</i>
	<i>pygopus schraderi</i>
	<i>Pygopus steelescotti</i>
Pythonidae	<i>Antaresia stimsoni</i>
Scincidae	<i>Acritoscincus duperreyi</i>

Carlia gracilis
Carlia triacantha
Cryptoblepharus egeriae
Cryptoblepharus pannosus
Cryptoblepharus
plagiocephalus
Ctenotus alacer
Ctenotus atlas
Ctenotus brooksi
Ctenotus decaneurus
Ctenotus fallens
Ctenotus hebetior
Ctenotus helenae
Ctenotus joanae
Ctenotus lateralis
Ctenotus leae
Ctenotus leonhardii
Ctenotus olympicus
Ctenotus pantherinus
Ctenotus quattuordecimlineatus
Ctenotus regius
Ctenotus robustus
Ctenotus saxatilis
Ctenotus schomburgkii
Ctenotus strauchii
Ctenotus uber
Cyclodomorphus branchialis
Egernia depressa
Egernia stokesii
Emoia atrocostata
Emoia nativitatis CR
Eremiascincus fasciolatus
Eremiascincus intermedius
Eremiascincus richardsonii
Hemiergis decresiensis
Hemiergis peronii
Lampropholis guichenot
Lerista bipes
Lerista bougainvillii
Lerista desertorum
Lerista labialis
Lerista macropisthopus
Lerista microtis
Lerista picturata
Lerista punctatovittata
Lerista timida
Liopholis inornata
Liopholis striata
Lygosoma bowringii
Menetia greyii
Morethia adelaidensis
Morethia boulengeri
Morethia lineocellata
Morethia taeniopleura
Niveoscincus metallicus
Niveoscincus ocellatus
Pseudemoia entrecasteauxii
Pseudemoia pagenstecheri
Tiliqua multifasciata
Tiliqua nigrolutea
Tiliqua occipitalis
Tiliqua rugosa
Tiliqua scincoides

	Typhlopidae	<i>Ramphotyphlops bicolor</i> <i>Ramphotyphlops bituberculatus</i> <i>Ramphotyphlops endoterus</i> <i>Ramphotyphlops grypus</i> <i>Ramphotyphlops guentheri</i> <i>Ramphotyphlops hamatus</i> <i>Ramphotyphlops ungirostris or ligatus</i>
	Varanidae	<i>Varanus acanthurus</i> <i>Varanus caudolineatus</i> <i>Varanus giganteus</i> <i>Varanus glebopalma</i> <i>Varanus gouldii</i> <i>Varanus panoptes</i> <i>Varanus scalaris</i> <i>Varanus spenceri</i> <i>Varanus storri</i> <i>Varanus tristis</i>
	Chelidae	<i>Chelodina longicollis</i> <i>Emydura krefftii</i>
Frogs Anura	Hylidae	<i>Cyclorana alboguttata</i> <i>Cyclorana novaehollandiae</i> <i>Litoria caerulea</i> <i>Litoria cyclorhyncha</i> <i>Litoria ewingii</i> <i>Litoria latopalmata</i> <i>Litoria moorei</i> <i>Litoria peronii</i> <i>Litoria rubella</i>
	Myobatrachidae	<i>Crinia signifera</i> <i>Heleioporus eyrei</i> <i>Heleioporus psammophilus</i> <i>Limnodynastes dorsalis</i> <i>Limnodynastes dumerilii</i> <i>Limnodynastes fletcheri</i> <i>Limnodynastes ornatus</i> <i>Limnodynastes tasmaniensis</i> <i>Limnodynastes terraereginae</i> <i>Neobatrachus centralis</i> <i>Neobatrachus pictus</i> <i>Opisthodon spenceri</i>
Birds	Acanthizidae	<i>Acanthiza chrysorrhoa</i> <i>Acanthiza pusilla</i> <i>Acanthiza reguloides</i> <i>Sericornis frontalis</i> <i>Smicrornis brevirostris</i>
	Accipitridae	<i>Aquila audax</i> <i>Milvus migrans</i>
	Aegothelidae	<i>Aegotheles cristatus</i>
	Alaudidae	<i>Mirafrja javanica</i>
	Anatidae	<i>Anas castanea</i> <i>Anas gibberifrons</i> <i>Anas rhynchotis</i> <i>Aythya australis</i> <i>Chenonetta jubata</i>
	Apodidae	<i>Collocalia esculenta</i>
	Ardeidae	<i>Nycticorax caledonicus</i>
	Artamidae	<i>Artamus cinereus</i> <i>Cracticus nigrogularis</i> <i>Cracticus tibicen</i> <i>Cracticus torquatus</i>

Cacatuidae	<i>Cacatua sanguinea</i> <i>Callocephalon fimbriatum</i> <i>Eolophus roseicapillus</i> <i>Nymphicus hollandicus</i>	
Charadriidae	<i>Charadrius bicinctus</i> <i>Charadrius ruficapillus</i>	
Columbidae	<i>Chalcophaps indica</i> <i>Columba livia</i> <i>Ducula whartoni</i> <i>Geopelia cuneata</i> <i>Ocyphaps lophotes</i> <i>Phaps chalcoptera</i> <i>Phaps elegans</i> <i>Streptopelia chinensis</i>	NT
Corcoracidae	<i>Corcorax melanorhamphos</i> <i>Struthidea cinerea</i>	
Corvidae	<i>Corvus</i> sp.	
Dromaiidae	<i>Dromaius novaehollandiae</i>	
Estrildidae	<i>Neochmia temporalis</i> <i>Poephila bichenovii</i> <i>Stagonopleura oculata</i> <i>Taeniopygia guttata</i>	
Fringillidae	<i>Carduelis carduelis</i> <i>Carduelis flammea</i>	
Glareolidae	<i>Pratincole</i> sp.	
Halcyonidae	<i>Todiramphus sanctus</i>	
Hirundinidae	<i>Hirundo neoxena</i>	
Iridopidae	<i>Petrochelidon nigricans</i>	
Laridae	<i>Larus dominicanus</i>	
Locustellidae	<i>Cincloramphus cruralis</i>	
Maluridae	<i>Malurus cyaneus</i> <i>Malurus lamberti</i> <i>Malurus leucopterus</i>	
Megapodiidae	<i>Leipoa ocellata</i>	VU
Meliphagidae	<i>Acanthorhynchus tenuirostris</i> <i>Anthochaera carunculata</i> <i>Epthianura tricolor</i> <i>Lichenostomus chrysops</i> <i>Lichenostomus ornatus</i> <i>Lichenostomus penicillatus</i> <i>Lichenostomus virescens</i> <i>Manorina flavigula</i> <i>Manorina melanocephala</i> <i>Philemon corniculatus</i> <i>Phylidonyris novaehollandiae</i>	
Monarchidae	<i>Grallina cyanoleuca</i>	
Motacillidae	<i>Anthus novaeseelandiae</i> <i>Anthus richardi</i>	
Pachycephalidae	<i>Oreoica gutturalis</i> <i>Pachycephala pectoralis</i> <i>Pachycephala rufiventris</i>	
Pardalotidae	<i>Aphelocephala leucopsis</i> <i>Pardalotus punctatus</i> <i>Pardalotus striatus</i>	
Passeridae	<i>Passer domesticus</i>	
Petroicidae	<i>Eopsaltria australis</i> <i>Petroica goodenovii</i> <i>Petroica multicolor</i> <i>Petroica phoenicea</i>	NT
Phalacrocoracidae	<i>Leucocarbo atriceps</i> <i>purpurascens</i>	
Phasianidae	<i>Coturnix pectoralis</i> <i>Coturnix ypsilophora</i>	

	Podargidae	<i>Podargus strigoides</i>	
	Procellariidae	<i>Pachyptila desolata</i> <i>Pachyptila turtur</i> <i>Pterodroma lessonii</i> <i>Puffinus tenuirostris</i>	
	Psittaculidae	<i>Alisterus scapularis</i> <i>Barnardius zonarius</i> <i>Melopsittacus undulatus</i> <i>Neophema pulchella</i> <i>Northiella haematogaster</i> <i>Platycercus elegans</i> <i>Platycercus eximius</i> <i>Polytelis anthopeplus</i> <i>Psephotus haematonotus</i> <i>Psephotus varius</i>	
	Ptilonorhynchidae	<i>Ptilonorhynchus violaceus</i>	
	Rallidae	<i>Porzana</i> sp. <i>Gallirallus australis</i> <i>Tribonyx mortierii</i>	VU
	Recurvirostridae	<i>Cladorhynchus leucocephalus</i>	
	Rhipiduridae	<i>Rhipidura fuliginosa</i> <i>Rhipidura leucophrys</i> <i>Rhipidura rufifrons</i>	
	Scolopacidae	<i>Arenaria interpres</i> <i>Calidris ruficollis</i>	
	Spheniscidae	<i>Aptenodytes patagonicus</i> <i>Eudyptes chrysocome</i> <i>Eudyptes schlegeli</i> <i>Eudyptula minor</i>	VU
	Sturnidae	<i>Acridotheres tristis</i> <i>Sturnus vulgaris</i>	
	Turdidae	<i>Turdus merula</i> <i>Turdus poliocephalus</i> <i>Zoothera dauma</i>	
	Turnicidae	<i>Turnix castanotus</i> <i>Turnix pyrrhothorax</i> <i>Turnix varius</i> <i>Turnix velox</i>	
	Tytonidae	<i>Tyto alba</i>	
	Zosteropidae	<i>Zosterops lateralis</i> <i>Zosterops natalis</i>	
Invertebrates	Class	Order	
	Arachnida	Araneae Scorpiones	
	Chilopoda	-	
	Insecta	Blattodea Coleoptera Dermaptera Diptera Hemiptera Hymenoptera Lepidoptera Mantodea Neuroptera Odonata Orthoptera Phasmatodea Plecoptera	
	Malacostraca	Decapoda Pedunculata	

Reference: IUCN (2013) *The IUCN Red List of Threatened Species. Version 2013.2*. Available at: <http://www.iucnredlist.org/>.

Appendix C.

GPS collaring of feral cats

Introduction

Domestic cats *Felis catus* have established self-sustaining feral populations in urban and non-urban areas around the world (Long 2003; Chapter 2) where they cause extensive damage to native fauna (Medina et al. 2011; Woinarski et al. 2015). Programmes aimed at reducing the impacts of feral cats generally use lethal control, such as shooting, trapping or poison baiting, to reduce cat population densities (Fisher et al. 2014b). Given the generally high effort and cost associated with these programmes (Zuberogitia et al. 2010; Fisher et al. 2014b), it is important to consider how such approaches can be optimised. Information on predator spatial ecology is an important precursor to effective control programmes, and such information can help determine the density at which control devices should be deployed (Moseby et al. 2009b; Carter et al. 2011), which habitat types should be targeted (Recio et al. 2010; Bengsen et al. 2012), and the overall scale of control operations (Mosnier et al. 2008). The aim of this component was to study the spatial ecology of feral cats in a semi-arid environment using GPS-tracking collars. I sought to quantify cat home range sizes, movement patterns and habitat selection, and use this information to improve the management of feral cats in the study landscape and elsewhere.

Methods

Feral cat trapping

Feral cats were trapped at Charles Darwin Reserve (see Chapter 1 for study site description) using padded leg-hold traps (Victor 'Soft Catch' traps no. 3; Woodstream Corporation, Lititz, Pennsylvania) over a period of three weeks in March 2013 at 130 trap sites (Table C.1, Figure C.1). Traps were set in pairs inside a corral bordered by vegetation with a lure of cat faeces and urine to guide the cats over the trigger plates. At any one time, up to fifty pairs of traps were set beside access tracks, separated by at least 750 m each (Figure C.1).

Traps were checked starting at sunrise each morning and again in the afternoon. Captured cats were sedated with an intramuscular injection of Zoletil® 100 (Virbac, Milperra, Australia) to the hind limb. Once sedated, cats were checked for trap injuries, sexed, weighed, and an assessment of their body condition was made. We also classed animals as either adult, sub-adult or juvenile based on size, weight and degree of tooth wear. Fourteen cats were fitted with a 120 g GPS/VHF radio collar with a timed-released mechanism (Telemetry Solutions, Concorde, USA). Only cats with a body mass of ≥ 2.4 kg were collared, which restricted collar weight to $< 5\%$ of body mass. Eleven of the collars were programmed to attempt a GPS fix every 150 minutes and to fall off the animals on June 30 2013, approximately three months after deployment. The remaining three collars were programmed to take a fix every 12 minutes and were programmed to fall off the animal after 10 days. Procedures for the capture, handling and collaring of cats were approved by the Edith Cowan University Animal Ethics Committee (project 8669).

Animal tracking

I conducted radio tracking to check the status and location of the collared animals every two to three weeks after deployment, except for the month of June when no tracking was undertaken (Table C.1). I scanned the collar frequencies using a three-element Yagi antenna and a VHF receiver while travelling by vehicle along access tracks. This involved either stopping every 500 m and standing on the vehicle while sweeping the antenna to increase range, or continuous scanning from the back of the vehicle while travelling at ~ 5 km h⁻¹. I did not attempt to triangulate any locations as I was only interested in the general location of the animals and whether the collar was emitting the mortality signal.

In April and May, I undertook targeting radio tracking to locate the collars of those three animals (M04, M06, F12) that were fitted with collars programmed to fall off after 10 days of operation (Table C.1). This involved 6 hours of tracking in the vicinity of the three capture locations over April 9-12th. I also undertook ground-based searches around the capture location of F12 on May 22nd and 23rd. During these searches I continually searched for the frequency of all collars. Then

in July 2013 I used a light aircraft to locate the remaining collars after the programmed drop-off date of 30th June (Table C.1). The aircraft was a Cessna 172N with dual antennas connected to a hand receiver. The aircraft flew along linear transects separated by 1 km at 80 knots, 1,000 feet above ground level. Tracking was undertaken for 2 hours on July 5th and 3 hours on July 6th, most parts of the study area were covered twice. If a collar signal was detected from the air, a GPS reading was taken and this point was later navigated to on foot and the surrounding area was searched using the handheld antenna and receiver. Additional vehicle-based radio tracking was undertaken from July 12th to 15th (Table C.1) using an antenna attached to a rotating tower on the tray of a vehicle at a total height of 3.5 m above the ground. Access tracks were driven at ~5 km h⁻¹ while one person stood on the vehicle tray, slowly rotating the antenna in a 300° arc with the receiver set to the scan setting.

Table C.1 Summary of capture and tracking efforts for feral cats.

Date	Method	Notes
March 10-31	Leg-hold trapping	14 animals fitted with GPS collars
April 9-12	Vehicle-based tracking	-
May 3	Tracking by vehicle and on foot	-
May 13	Vehicle-based tracking	-
May 22	6.5 km loop on foot	West of F12 capture location
May 23	4 km loop on foot	East of F12 capture location
July 5-6	Aerial radio tracking	Plane detected signals of M11, M04
July 5	1 km loop on foot	Searched location of M11
July 6	6.1 km loop on foot	Searched location of M04
July 12-15	Vehicle-based tracking	F13 detected near Sandplain Junction
August 10-18	Leg-hold trapping	-

Results and Discussion

Study animals

Traps were open for a total of 992 trap nights in March and each trap site was operational for between 1 and 13 days (mean = 7.6). I captured 16 cats and the trap rate was 1.6 cats per 100 trap nights. The animals consisted of 11 adult males, three sub-adult females, one adult female and one juvenile female (Table C.2). The mean weight of males was 3.85 kg ($SE = 0.15$) and the mean weight of all females was 2.36 kg ($SE = 0.22$), or 2.58 kg ($SE = 0.09$) excluding the juvenile. One animal (F99) was too small for collaring and was released, and a second animal (M99) was euthanased because it suffered a trap injury on its leg (Table C.2).

Table C.2 Summary of feral cats that were captured during the March 2013 trapping exercise at Charles Darwin Reserve.

ID code	Date	Sex ^A	Age class ^B	Weight (kg)	Coat colour	Notes
M01	13/03	M	A	3.90	Black	--
M08	13/03	M	A	3.80	Black	--
M07	13/03	M	A	4.05	Grey tabby	--
M09	14/03	M	A	4.90	Black	--
F10	15/03	F	SA	2.50	Grey tabby	--
F99	17/03	F	J	1.50	Grey tabby	Too small for collaring
F13	18/03	F	SA	2.40	Grey tabby	--
M03	18/03	M	A	3.80	Grey tabby	--
F14	25/03	F	A	2.60	Grey tabby	--
M05	26/03	M	A	4.20	Grey tabby	--
M99	28/03	M	A	3.40	Grey tabby	Euthanased
M02	29/03	M	A	3.20	Grey tabby	--
M11	29/03	M	A	3.20	Black	--
M06	30/03	M	A	3.70	Grey tabby	--
F12	31/03	F	SA	2.80	Grey tabby	--
M04	31/03	M	A	4.20	Grey tabby	--

^A M, male; F, female.
^B A, adult; SA, sub-adult; J, juvenile.

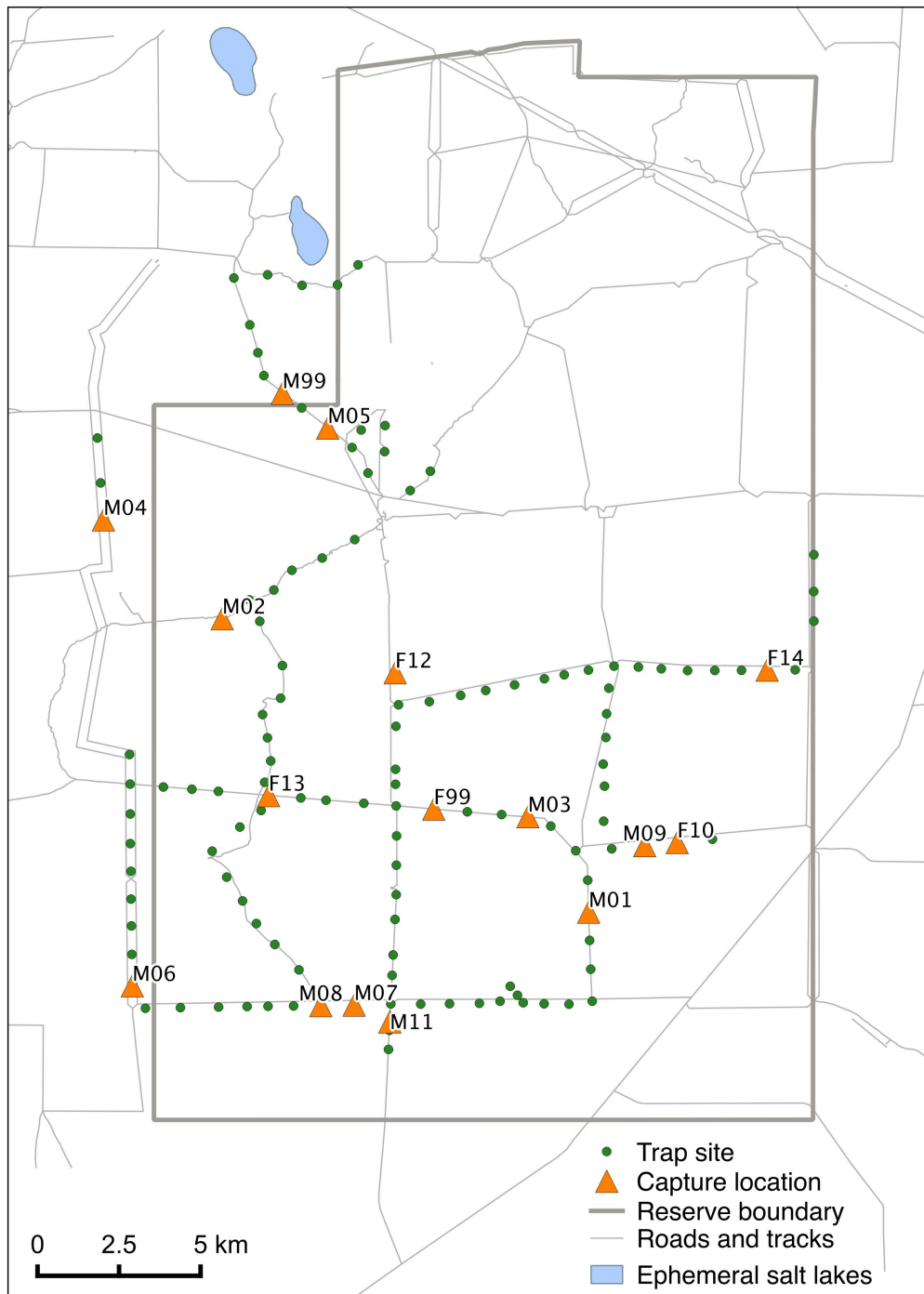


Figure C.1 Trap sites and capture locations of feral cats at Charles Darwin Reserve in March 2013.

Search effort

I did not detect the VHF signals of any animals during the vehicle- and ground-based tracking in April and May. In July 2013 the aircraft searched > 150,000 ha (Figure C.2), which is more than five times the size of the area containing the original capture locations (~30,000 ha maximum convex polygon). Despite the large search area, the plane detected the signal of only two of the 14 collared animals. On July 5th the plane detected the signal of animal M11 and that afternoon I searched the vicinity of this location (point A in Figure C.2) on foot by travelling a 1 km round-trip route into the bush. I was unable to detect any signal from the collar, despite the plane having detected the signal at that location just three hours earlier. The next day, the plane re-surveyed that same area, but was unable to detect M11's signal again. On July 6th, the plane detected signal from M04 (point B in Figure C.2) and I conducted a similar ground survey by walking a 6.1 km round-trip into the bush the same day, although I did not detect any signal from that collar either.

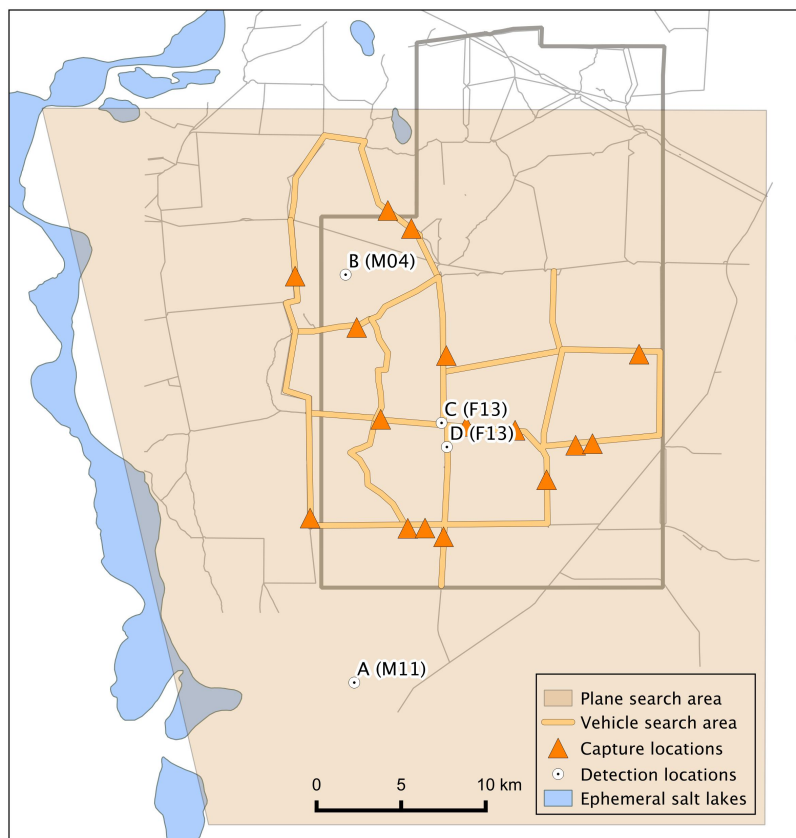


Figure C.2 Location of search areas covered by light aircraft and ground vehicle.

In a further attempt to locate any of the collars, I undertook vehicle-based tracking in July by conducting surveys starting at 1.5 hours before sunset until 2-4 hours after sunset using the rotating vehicle-mounted antenna. I covered each section of track around the capture locations (Figure C.2) at least twice at night and once during the day. Only one additional collar signal was detected: F13. I first detected this signal at 6:20 pm on July 12th, 800 m west of Sandplain Junction (point C in Figure C.2). It was not possible to follow the signal on foot at that time, as daylight had ended. However, I detected the same signal at 11:55 am the next day, 1.5 km south of Sandplain Junction and 1.8 km from the previous point of detection (point D in Figure C.2). I initially approached the signal via vehicle, and then on foot, but found that the strength and direction of the signal changed as I approached it. I searched the area for more than one hour, but eventually lost the signal. I was also unable to detect the signal again in the days that followed.

Discussion

Although 14 cats were fitted with GPS tracking collars in March 2013, no collars, nor any data, could be retrieved. There are two possible, non-exclusive explanations for this outcome: equipment failure, and inadequate search area. I will begin by discussing the size of the search area. The aircraft, which would of have a greater detection range than ground-based tracking⁵, searched a large area relative to the original capture locations (Figure C.2), but only detected two animals in that area. It is possible that some animals moved outside of this area between collaring and aerial radio tracking. For example, the plane detected the VHF signals of two animals (M11 and M04) 11 and 3 km from their original capture locations respectively. Previous studies have also recorded GPS-collared cats moving large distances; for example, in arid South Australia, the mean maximum distance between all locations for individual cats was 8.8 km, with one male cat moving > 45 km in two days, a second male moving > 26 km in three days and a third male moving > 20 km within 24 hours (Moseby et al. 2009b). The mean approximate distance between the cats' capture locations and the perimeter of the

⁵ The manufacturer reported a 500-m ground range for the collars' VHF transmitters, which considerably limited my ability to detect cats because most parts of the study site are between 1 and 5 km away from tracks and hence inaccessible by vehicle. Searches on foot are difficult in the dense shrubland that covers much of the study site.

plane's search area was 13.4 km (range: 7.5 – 18). Although the current study site is less arid than that of Moseby et al. (2009b) and hence cats would be expected to range shorter distances (Liberg et al. 2000), some cats may have dispersed outside of the area searched by the plane and hence not been detected in the searches. This possibility was not planned for in advance and it was not possible to undertake further aerial radio tracking at that time because only a limited amount of fuel was available on site. I later decided not to conduct additional aerial radio tracking because I had been unable to locate on the ground those two collars that the plane had detected during the first round of tracking. I deemed the risk of failure disproportionate to the financial cost. Also, stalking and shooting of any cats tracked on the ground was deemed unlikely to be successful given the inaccessibility of the dense shrubland thickets that cover much of the study area.

Remote camera monitoring indicated a decline in cat activity in the southern part of the reserve between February and May, and May and August 2013 (see Appendix D). The reason for this decline is unclear, although it occurred after I had fitted the GPS collars to the cats in March 2013, most of them in that same general area. I also conducted follow-up leg-hold trapping in August 2013 in an attempt to recapture any collared animals. I used different lures to the first round of trapping to reduce the possibility that previously captured cats would avoid the traps. The lures were a commercial scent-based lure 'Catastrophe' (Outfoxed Pest Control, Ivanhoe, VIC, Australia) and Felid Attracting Phonics (Westcare Industries, Bassendean, WA, Australia), which are audio lures that emit the sound of a cat meowing. Traps were open for between seven and nine nights at 49 sites and I only captured one cat (a new male animal), which was then euthanased. Trap success was 0.25 cats per 100 trap-nights (cf. 1.6 in March), which supports the low cat activity as recorded by remote cameras around that time and the possibility that some of the collared cats had moved outside of that area.

The second possible explanation relates to equipment failure. Retrieval of the collars depended on successful operation of the inbuilt drop-off mechanisms. Since I was unable to retrieve any of the collars, I cannot say with certainty whether the drop-off mechanisms worked correctly or not. However, three pieces of evidence suggest that the drop-off mechanisms on at least some collars did not

work successfully. Firstly, the plane detected the VHF signal of animal M11, but I was unable to relocate the signal in that area on the same day, nor was the plane able to detect it again the next day. Similarly, I was unable to detect the signal of animal M04 in the area that the plane detected it earlier that day. Finally, I detected the VHF signal of animal F13 on the evening of July 12th and again during the day on July 13th. I attempted to home in on that signal on foot, but the strength and direction of the signal changed as I approached it. These observations suggest that the collars were moving and hence were likely still attached to the animals. Extensive discussions with the manufacturer, Telemetry Solutions, resulted in no resolution as to whether equipment failure may have occurred. The ultimate fate of the animals and GPS collars remains unknown.

Appendix D.

Response of feral cats to a track-based baiting programme using *Eradicat*[®] baits

Doherty TS and D Algar (2015) *Response of feral cats to a track-based baiting programme using Eradicat[®] baits*. *Ecological Management & Restoration*, 16:124–130.

Introduction

The feral cat *Felis catus* preys on native fauna and is responsible for numerous extinctions globally (Medina et al. 2011; Woinarski et al. 2015). Predation by feral cats can jeopardise conservation programmes aiming to reintroduce native fauna into areas of their former range (Moseby et al. 2011b; Potts et al. 2012), and cats can have nonlethal impacts on susceptible populations through competition, disease transmission, induced predator avoidance behaviour and hybridisation (Daniels et al. 2001; Fancourt & Jackson 2014; Medina et al. 2014). Cats have been particularly damaging to Australian wildlife and, together with the introduced European red fox *Vulpes vulpes*, have contributed to the extinction of 22 Australian mammals since European settlement (Johnson 2006; Woinarski et al. 2014). Cats are considered to be a contributing factor to recent declines in northern Australia's mammal fauna (Woinarski et al. 2011; Fisher et al. 2014a; Ziembicki et al. 2015; Woinarski et al. 2015) and are listed as a *Key Threatening Process* under the Commonwealth *Environment Protection and Biodiversity Conservation Act 1999* (Department of the Environment Water Heritage and the Arts 2008). Reducing their impact is considered an essential action for the conservation of Australian birds and mammals (Denny & Dickman 2010; Woinarski et al. 2011; Garnett et al. 2013; Woinarski et al. 2014).

Techniques for controlling populations of feral cats include shooting, trapping, poison baiting and exclusion fencing (Denny & Dickman 2010). Cats have successfully been eradicated from a number of islands (DIISE 2014) and fenced mainland reserves using different combinations of control methods. Unfenced mainland sites, on the other hand, require sustained control efforts because cats

have a high reproductive output and an aptitude for reinvasion (Read & Bowen 2001; Short & Turner 2005). Both trapping and shooting are time- and labour-intensive methods of pest control, whereas baiting is comparatively more cost effective when targeting larger areas (Fisher et al. 2014b). However, poison baiting of feral cats is notoriously challenging. While the red fox, dingo *Canis dingo* and dingo/dog *Canis lupus familiaris* hybrids ('wild dogs' hereafter⁶), will readily take carrion, inclusive of poison meat baits, inanimate baits are assumed to be less preferred food items relative to normal live prey for feral cats (Fisher et al. 2014b). However, feral cats are adaptable enough to scavenge, so where possible baiting should be timed to coincide with low availability of natural prey resources (Short et al. 1997; Algar et al. 2007; Moseby & Hill 2011; Christensen et al. 2013). Risbey et al. (1997) found that four different bait mediums (dried meat baits, a fishmeal-based bait, a bait coated in a flavour enhancer, and baited European rabbit *Oryctolagus cuniculus* carcasses) were all ineffective in controlling feral cats at Shark Bay in Western Australia. Other studies also found that dried meat baits were ineffective in controlling cats in arid and semi-arid Western Australia (Burrows et al. 2003; Algar & Burrows 2004). However, using fresh meat baits, Burrows et al. (2003) were able to reduce cat abundance in Western Australia's Gibson Desert by 75% and 100% during two years of below average rainfall.

The Western Australian Department of Parks and Wildlife (and its predecessors) has developed a bait medium and baiting technique that can effectively reduce feral cat populations, as well as fox and wild dog populations. The bait (*Eradicat*[®]) is similar to a chipolata sausage and is composed of 70% kangaroo meat mince, 20% chicken fat and 10% digest and flavour enhancers (Algar et al. 2007; Algar et al. 2013). It weighs approximately 20 g wet-weight, is dried to 15 g, blanched and then frozen (Algar et al. 2013). The toxic baits contain 4.5 mg of sodium monofluoroacetate (compound 1080) per bait. Uptake of *Eradicat*[®] by cats was significantly greater than uptake of both a chicken sausage bait and a dead day-old cockerel at a semi-arid site (Algar et al. 2007). The Department of Parks and Wildlife currently bait a number of locations in Western Australia by deploying *Eradicat*[®] baits from an aircraft at a rate of 50 baits km⁻²

⁶ The use of this term was requested by a journal reviewer, although the 'wild dogs' referred to here are the same animals as the 'dingoes' mentioned elsewhere in the thesis.

during late autumn or early winter, when prey availability is lowest and cats are more likely to consume the baits (Algar et al. 2011; Christensen et al. 2013; Algar et al. 2013). Field trials have shown that annual aerial baiting using *Eradicat*[®] can achieve sustained control of feral cats at the landscape scale (Algar et al. 2013). However, the efficacy of track-based baiting—where baits are laid by hand along roads or tracks—has not been tested, despite its potential utility to smaller landholders, such as private conservation organisations, given that it is less costly than aerial baiting over smaller areas. In this study, we measured the population response of feral cats to a track-based baiting programme using *Eradicat*[®] baits in the semi-arid northern Wheatbelt region of Western Australia. The study was operational in nature, rather than experimental, and hence did not involve replication of treatment and control areas.

Methods

Study site

We conducted this study at Charles Darwin Reserve (CDR), a ~68,000 ha pastoral lease 350 km north-east of Perth (29° 35' S, 116° 58' E), managed for conservation by Bush Heritage Australia and destocked of goats *Capra hircus* and sheep *Ovis aries* since 2003. The climate is semi-arid Mediterranean, with cool winters, hot summers and unreliable, low rainfall (mean 306 mm year⁻¹ at the adjacent Wanarra pastoral station; Bureau of Meteorology 2014). Dense mixed-species shrublands on yellow sandplains comprise 50% of the reserve's area, and the remainder is a mixture of eucalypt woodlands and other vegetation types (Braun 2006).

Poison baiting

Prior to the start of this trial, dried meat 1080 poison baits were laid on the reserve biannually, primarily for the control of foxes, although wild dogs are also likely to have taken those baits. That baiting programme ceased in March 2012 and no data are available on its efficacy. Poison baiting for feral cats using *Eradicat*[®] baits was conducted at CDR by Bush Heritage Australia in 2013 and 2014 under an experimental permit (PER14102) issued by the Australian Pesticides and Veterinary Medicines Authority, which only allowed baits to be laid once per year. Prior to being laid, baits were thawed and placed in direct sunlight – a process

termed 'sweating' – which causes the oils and lipid-soluble digest material to exude from the surface of the bait. During the sweating process, baits were sprayed with *Coopex*[®] insecticide at a concentration of 12.5 g L⁻¹ to deter ants from consuming the bait, which can make them less attractive to cats.

Baits were laid by hand from the back of a slow-moving vehicle at a rate of one bait every 50 m along access tracks in the southern half of the reserve (Figure D.1). This interval was chosen to maximise the baiting density that could be achieved and increase the likelihood of individual cats encountering baits when hungry (Algar et al. 2007; Algar et al. 2014). Baits were laid on alternate sides of tracks. Baiting was conducted on two occasions: 8th September 2013 and 11th May 2014, with 1,500 baits being laid on each occasion. Baiting in 2013 was planned to take place in May of that year, but delays in obtaining the research permit meant that the baiting was delayed until September. Baiting was only conducted when the local weather forecast predicted at least five consecutive days of dry weather because rain can make baits unpalatable to cats (Algar & Burrows 2004; Algar et al. 2013). Baiting density was ~11 baits km⁻² (if the baited area was taken as a minimum convex polygon around the baited tracks on the perimeter of the baiting envelope; Figure D.1).

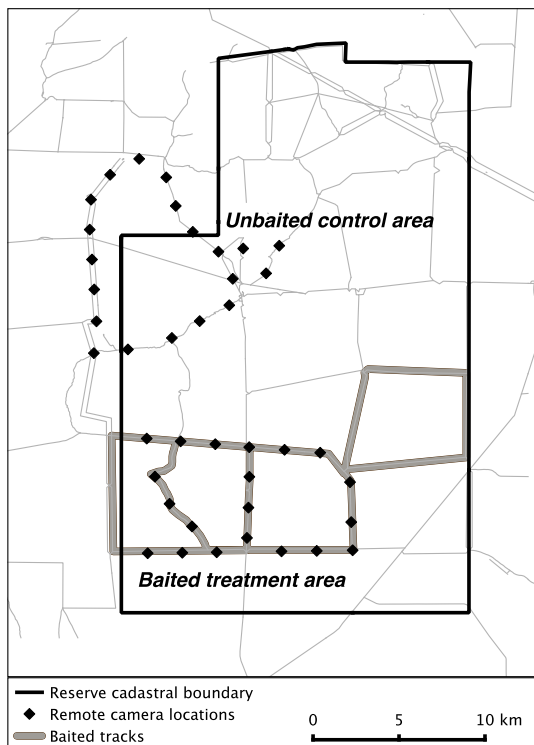


Figure D.1 Location of the baited part of the reserve (grey shaded tracks) and the 40 remote camera locations (black diamonds).

Predator monitoring

We used remote cameras in an unreplicated BACI design (before–after, control–impact) to monitor the response of predator ‘activity’ to baiting. Predator activity was surveyed using 40 remote cameras positioned on vehicle tracks (20 Moultrie i60 and 20 Scoutguard 560PV; Figure D.1). Twenty cameras, each separated by ≥ 2 km, were positioned on a circuit in the southern, baited part of the reserve, and 20 cameras were positioned on a northern circuit that was not subject to baiting and acted as an experimental control (Figure D.1). In studies such as this one, it is recommended that a single model of remote camera be used to reduce variation in detectability between individual cameras (Meek et al. 2015); however, financial constraints meant that we had to use two different camera models. Nevertheless, our approach to deploy equal numbers of the two camera types in treatment and control areas and randomly assign cameras to locations minimised any potential bias. The minimum distance between the northern cameras and the baited area was 5.5 km, although most northern cameras (75%) were > 9.5 km from the baited area. Mean feral cat home range estimates from similar environments in Australia were 2.48 km² (Molsher et al. 2005), 4.7 km² (Jones & Coman 1982), 5.11 km² (Bengsen et al. 2012), 9.8 km² (Hilmer 2010) and 22.1 km² (Edwards et al. 2001), which correspond to home range diameters between 1.8 and 5.3 km (if the home range is assumed to be a circle). The distance between our baited treatment and unbaited control areas is therefore sufficiently large enough for the two areas to be considered independent of each other for the purposes of this study, although we acknowledge that cats have occasionally been recorded moving larger distances in other parts of Australia (e.g. Moseby et al. 2009b).

Cameras were fixed to a steel post so that the sensor was ~ 30 cm above the ground and were programmed to take a series of three photographs each time the sensor was triggered, with a minimum delay of one minute between triggers because this was the minimum delay possible for one of the camera models (Moultrie). At half of the cameras, a raw chicken wing encased in a PVC bait holder pegged to the ground was used as a scent lure, and at the remaining cameras, an electronic device that makes the sound of a bird tweeting was used as an audio lure (Lucky Duck, WI, USA). Lures were swapped between cameras halfway

through each monitoring period. A fresh chicken wing was placed inside the bait holder each time the lures were swapped.

Cameras were operated for between 30 and 39 days immediately before each baiting event and again beginning 24 days after baiting in 2013 and 10 days after baiting in 2014 (Table D.1). Cameras were also operated for 11 days in February 2013 and 28 days in May/June 2013, independent of any baiting events (Table D.1).

Table D.1 Dates of remote camera monitoring sessions and baiting events.

Session	Survey length (days)	Sampling effort (camera-nights)	Notes
February 2013	11	370	One control camera malfunctioned
May 2013	28	1070	-
August 2013	30	1111	Two treatment cameras stolen
<i>Baiting</i> 8 th Sept.	-	-	-
October 2013	38	1106	One treatment camera malfunctioned
April 2014	39	1347*	-
<i>Baiting</i> 11 th May	-	-	-
May 2014	30	965*	One control malfunctioned

* NB: the difference between sampling effort pre- and post-baiting in 2014 is due to one control camera that malfunctioned for the entire post-baiting period and three other control cameras in which the batteries failed after between two and six days of operation also during the post-baiting period. These differences do not affect our interpretations of the effect of baiting because all of those cameras were in the unbaited control area.

Bait uptake trials

We also used the same remote cameras and settings to determine what animal species were responsible for removing baits. During laying of baits, we placed an *Eradicat*[®] bait in front of 18 cameras in September 2013 and 19 cameras in May 2014. Cameras were active for 2 weeks, and baits were not replaced if they were removed. No other lures were present at cameras during this time. Memory cards were collected from cameras after 2 weeks and photographs were inspected to determine whether baits were taken and what species were responsible. We classed a bait as 'not taken' if it was still present after the two-week period.

Statistical analyses

Remote camera photographs were stored in a database and tagged with the camera identification number, treatment (baited or unbaited), session, date, time and species using EXIFPro 2.0 (Kowalski & Kowalski 2012). Tags were written to the EXIF data of each file and then exported from EXIFPro as a text file. To ensure independence of repeat photographs of the same species caught on the same camera, we classified photographs that were captured within 15 min of each other as a single photograph ‘event’. Inspection of frequency tables of the time elapsed between photographs indicated that this was a suitable breakpoint (Table D.2). For each session, we summed the total number of independent photograph events of each species at each remote camera.

Table D.2 Percentage of feral cat photo events in time periods for the number of minutes between successive photos on the same camera within each session.

Time period (mins)	Percentage of photos
0 to 15	80.29
16 to 30	0.00
31 to 100	0.36
101 to 500	2.92
500 to 40,000	16.42

We used Poisson generalised linear mixed models to test the effect of baiting on feral cat activity. Foxes were rarely detected at the study site, and wild dogs were infrequently detected in the baited area (< 6% of photographs), so we did not analyse that data due to the small sample sizes. We used the number of photographs of cats caught on each camera in each session as the response variable and used the number of nights cameras were active (‘camera-nights’) as an offset to account for variable sampling effort. We fitted models with fixed effects of time (before/after) and treatment (baited/unbaited), the interaction term, and random intercepts for camera ID and model. Fitting camera model as a random intercept accounts for any additional variation associated with the two types of cameras (Moultrie or Scoutguard). We fitted separate models for the 2013 and 2014 baiting. An effect of baiting on cat activity would be shown as a significant interaction between time and treatment in the models. We calculated 95% confidence intervals (*CI*) for each predictor variable and inferred ‘significant’

effects where the confidence intervals did not overlap zero. For graphical representation, we standardised remote camera data to a relative activity index by dividing the number of photograph events on each remote camera by the number of camera-nights and multiplied this by 100. Models were fitted using the lme4 package version 1.1-6 in R version 3.0.2 (R Core Team 2013; Bates et al. 2014).

Results

Across the six monitoring periods, we captured 128 independent photographs of feral cats, 51 of wild dogs and four of foxes. Cat activity in the baited treatment area declined between February and August 2013, before baiting began, whereas it was relatively constant in the unbaited control area during the same period (Figure D.2).

Effect of baiting

In 2013, there was a significant treatment effect (Table D.3), with cat activity in the unbaited area being significantly higher than the baited area both before and after baiting (Table D.4; Figure D.3a). There was no significant change in cat activity following baiting in either the baited or unbaited areas (Table D.3, Figure D.3a). In the baited area, cats were detected on 5.6% of cameras prebaiting and 10.5% postbaiting, whereas cats were detected on 50% of cameras both before and after baiting in the unbaited control area (Table D.5). In 2014, there was a significant interaction between time and treatment (Table D.3), with an 85% decline in cat activity in the treatment area following baiting (Table D.4, Figure D.3b) and an 80% decline in the number of cameras detecting cats (Table D.5). In the unbaited control area, there was a small nonsignificant increase in cat activity following baiting (Table D.4, Figure D.3b), although the number of cameras detecting cats decreased slightly (Table D.5).

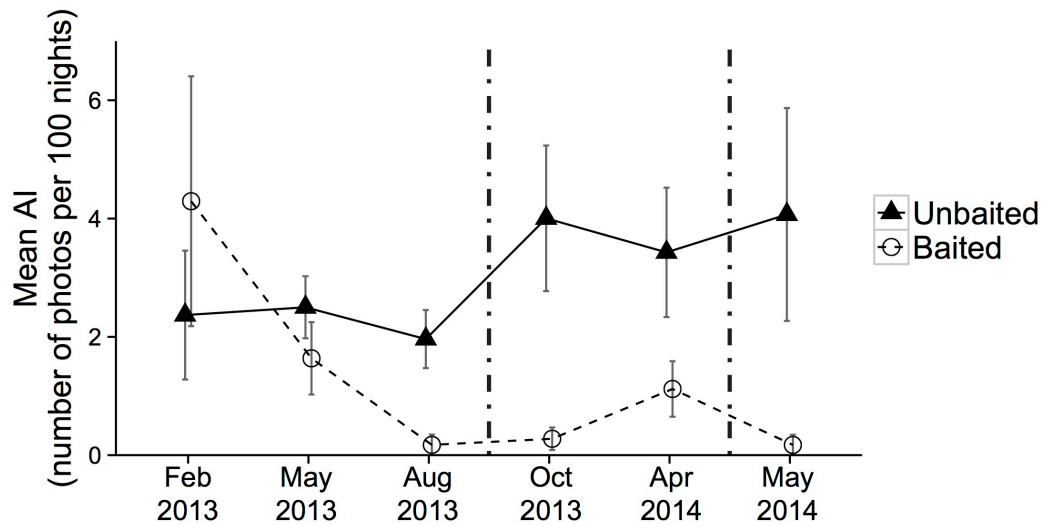


Figure D.2 Mean cat activity (number of photographs per 100 nights) and standard error bars in the unbaited control (solid line and triangles) and baited treatment (dashed line and circles) areas during six sampling periods. The dashed vertical lines indicate the timing of baiting in September 2013 and May 2014.

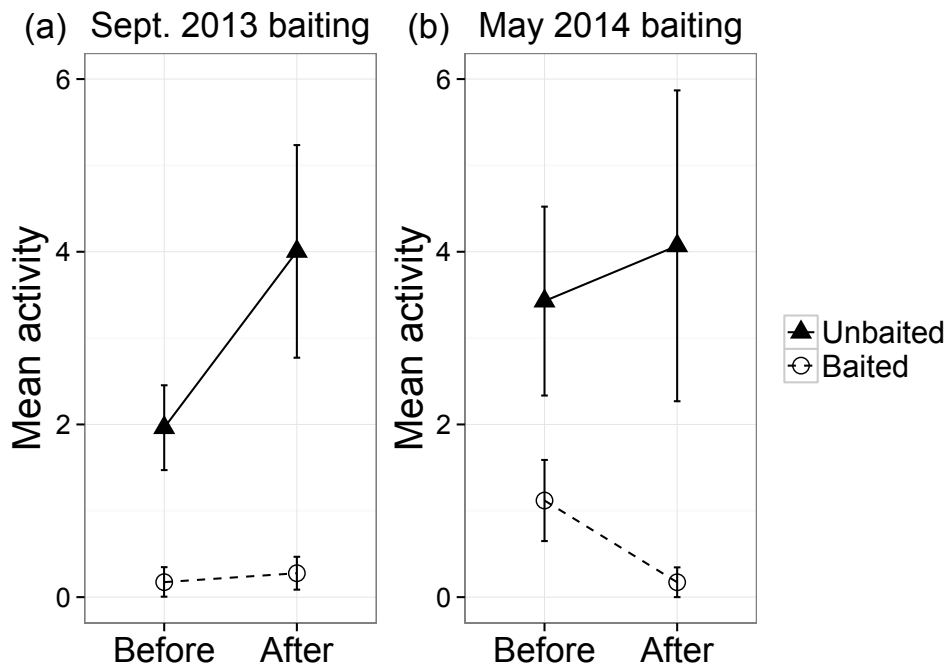


Figure D.3 Response of cat activity (number of photographs per 100 nights) to time (before/after) and treatment (baited/unbaited) in (a) September 2013 and (b) May 2014. Standard error bars are shown.

Table D.3 Mixed modelling results for the effect of time, treatment and the interaction term on cat activity at the September 2013 and May 2014 baiting events. Significant terms are indicated with bold text.

	Model term	Estimate	95% CI
September 2013	Time	-0.59	-1.30, 0.12
	Treatment	-2.26	-3.75, -0.77
	Time × Treatment	-0.07	-2.58, 2.43
May 2014	Time	-0.12	-0.71, 0.47
	Treatment	-3.05	-6.03, -1.22
	Time × Treatment	2.07	0.26, 5.04

Table D.4 Mean cat activity (number of photographs per 100 nights) in the baited treatment area and unbaited control area before and after baiting in September 2013 and May 2014. Standard errors are given in parentheses.

	Treatment	Pre-baiting	Post-baiting
September 2013	Baited	0.17 (0.17)	0.28 (0.19)
	Unbaited	1.96 (0.49)	4.00 (1.23)
May 2014	Baited	1.12 (0.47)	0.17 (0.17)
	Unbaited	3.43 (1.09)	4.07 (1.80)

Table D.5 Percentage of remote cameras in the baited treatment area and unbaited control area that detected feral cats before and after baiting in September 2013 and May 2014. Raw number of cameras is given in parentheses.

	Treatment	Pre-baiting	Post-baiting
September 2013	Baited	5.6% (1)	10.5% (2)
	Unbaited	50% (10)	50% (10)
May 2014	Baited	25% (5)	5% (1)
	Unbaited	50% (10)	42.1% (8)

Bait uptake trials

During the bait uptake trials, three cameras malfunctioned and the bait was not visible in the field of view of four other cameras, so we have excluded these seven baits from the results below. Of the remaining baits (n = 30), animals removed two-thirds and the remaining one-third were not taken, as evidenced by baits remaining *in situ* when cameras were checked. Corvids *Corvus* spp. removed 12 baits (40%), cats removed six (20%) and varanids *Varanus* spp. removed two (6.7%). Cats removed one bait in 2013 and five in 2014. All removed baits were taken within five days of being laid.

Discussion

We sought to determine whether track-based baiting using *Eradicat*[®] baits could effectively reduce feral cat activity at a semi-arid site in Western Australia. As this study took advantage of an operational baiting programme, there are certain limitations inherent in the study design and subsequent inferences. Specifically, baiting could only be conducted once per year, and control and treatment areas were not replicated. Nevertheless, the following findings are of value to future cat baiting trials.

The lack of a response to baiting in 2013 could be due to the existing low cat numbers in the baited area and/or the timing of the baiting. During 2013, cat activity had already declined in the baited area prior to the baiting event. The reason for this decrease is unclear, especially given that cat activity in the unbaited control area remained relatively stable during the same period. Despite this, even if cat numbers were high enough to detect any effect of baiting, it may have been compromised by the inappropriate timing. Cat baiting in Western Australia is timed to periods of lowest prey availability and hence when cats are most hungry and more likely to consume the baits (Short et al. 1997; Algar et al. 2007). Christensen et al. (2013) found that the efficacy of aerial cat baiting operations was negatively correlated with a predator–prey index, that is baiting was most effective when the number of prey available to a single cat was lowest. The period of lowest prey availability in the study region is in late autumn, when temperatures are cooler, but before the winter rainfall. The 2013 baiting took place in September, a time when juvenile rabbits would be entering the population and reptiles are more active due to the higher daily temperatures – both of which are key prey species for cats at the study site (Chapter 3). The increased prey availability at this time would likely have made cats less likely to consume the baits. In contrast, the 2014 baiting appeared to be effective in reducing cat activity. Baiting in 2014 was undertaken in May when prey availability is expected to be at its lowest.

Future considerations

An issue with track-based baiting is that tracks represent only a small proportion of the home range of a cat, and hence, cats may access tracks for only a relatively small proportion of their daily activity (Algar et al. 2007). Algar et al.

(2007) suggested that increasing baiting frequency at the time of lowest prey availability could improve the efficacy of track-based baiting because baits would be present at different times and thus increase the chances that cats are hungry when they encounter the baits. The experimental permit for this project allowed for only a single annual application of baits, but investigating the influence of increased baiting frequency on bait uptake by cats could be the focus of future track-based baiting work.

Additionally, the network of tracks at a site governs the potential baiting densities that can be achieved. Higher baiting densities can be achieved at sites with higher densities of tracks. We estimated our baiting density to be ~ 11 baits km^{-2} , whereas aerial baiting is conducted at 50 baits km^{-2} . However, our calculation did not include a buffer extending outside of the baiting envelope, nor did it consider the central areas of land that were up to 3.5 km from the nearest baited track. Although we do not have data on optimal baiting densities, track-based baiting may not be effective at sites that have a limited track network and consequently have large areas of land within which cats would be unlikely to encounter baits.

Nontarget bait uptake also has the potential to limit bait availability for cats. Corvids removed twice the number of baits than cats did in our bait uptake trials, and previous studies have also recorded relatively high rates of bait uptake by both corvids and varanids compared to cats (Algar et al. 2007; Denny 2009a; Denny 2009b; Moseby et al. 2011a). Although uncommon during our study, foxes and wild dogs also readily take *Eradicat*[®] baits (Burrows et al. 2003). We only recorded varanids removing two baits in our study and baiting during the cooler months when reptiles are less active is likely to reduce bait uptake by varanids. Additionally, placing baits under bushes rather than in the open may decrease uptake by corvids (Moseby et al. 2011a). Burying the baits is also likely to reduce non-target uptake, as has been observed in canid baiting programmes (Allen et al. 1989; Thomson & Kok 2002; Glen & Dickman 2003), although this is also likely to reduce bait uptake by cats. Cats are less likely than canids to locate and excavate buried baits because they are primarily auditory and visual hunters (Bradshaw 1992; Fisher et al. 2014b) that lack the acute olfactory senses of canids. Surface-laying of cat baits is standard practice in Western Australia (Algar et al. 2007; Algar

et al. 2011; Algar et al. 2013) where the native fauna have a relatively high tolerance to 1080 poison because they have co-evolved with endemic plants containing a similar compound (Twigg & King 1991; Twigg et al. 2003). Alternative means of bait presentation that reduce nontarget risk but maximise uptake by cats, such as suspending baits above the ground (Algar & Brazell 2008), should be investigated for use in other parts of Australia. Additionally, a prototype cat bait (*Curiosity*[®]) is being tested elsewhere in Australia (Johnston et al. 2011; Johnston et al. 2012; Johnston et al. 2013; Johnston et al. 2014), which encapsulates the poison in a pellet inside the bait and may reduce nontarget risks (Marks et al. 2006; Hetherington et al. 2007; Buckmaster et al. 2014).

Our results are based on two years of baiting trials, with one year potentially being compromised by seasonal effects. However, the significant reduction in cat activity following track-based baiting in the second year of the project is encouraging. As a result of this study, we make five key recommendations to help inform future cat baiting programmes and research: (i) baiting should be conducted during seasons of lowest prey availability; (ii) the effect of increased baiting frequency (during periods of low prey availability) should be investigated; (iii) the impact of nontarget uptake on bait availability to cats should be considered; (iv) innovative methods of bait presentation that minimise nontarget risks but maximise uptake by cats should be developed; and (v) spatially and temporally replicated experimental trials should be conducted.

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Co-author statements

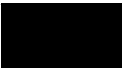
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Chapters 1 & 6


RE: Multiple threats, or multiplying the threats? Interactions between invasive predators and other ecological disturbances


To Whom It May Concern,


I, Tim S. Doherty, made the following contributions to the paper entitled 'Multiple threats, or multiplying the threats? Interactions between invasive predators and other ecological disturbances': conceived the original idea, collated and reviewed the literature, wrote the first draft, and led the writing and editing of the final manuscript.

Tim S. Doherty, Edith Cowan University.
Signature:  Date: 20 May 2015

I, as a co-author, endorse that this level of contribution by the candidate indicated above is appropriate.

Chris R. Dickman, University of Sydney.
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Dale G. Nimmo, Deakin University and Charles Sturt University.
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Euan G. Ritchie, Deakin University
Signature:  Date: 20 May 2015

Chapter 2

RE: A critical review of habitat use by feral cats and key directions for future research and management

To Whom It May Concern,

I, Tim S. Doherty, made the following contributions to the paper entitled 'A critical review of habitat use by feral cats and key directions for future research and management': conceived the original idea, collated and reviewed the literature, wrote the first draft, and led the writing and editing of the final manuscript.

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I, as a co-author, endorse that this level of contribution by the candidate indicated above is appropriate.

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Chapter 4

RE: Response of a shrubland mammal and reptile community to a history of landscape-scale wildfire

To Whom It May Concern,

I, Tim S. Doherty, made the following contributions to the paper entitled 'Response of a shrubland mammal and reptile community to a history of landscape-scale wildfire': collected most of the data, performed most of the analyses, wrote the first draft, and led the writing and editing of the final manuscript.

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I, as a co-author, endorse that this level of contribution by the candidate indicated above is appropriate.

Robert A. Davis, Edith Cowan University.

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Chapter 5

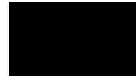
RE: A game of cat-and-mouse: microhabitat influences rodent foraging in recently burnt, but not long unburnt shrublands

To Whom It May Concern,

I, Tim S. Doherty, made the following contributions to the paper entitled 'A game of cat-and-mouse: microhabitat influences rodent foraging in recently burnt, but not long unburnt shrublands': conceived the original idea, designed the study, collected and analysed the data, wrote the first draft, and led the writing and editing of the final manuscript.

Tim S. Doherty, Edith Cowan University.

Signature:



Date: 27 April 2015

I, as a co-author, endorse that this level of contribution by the candidate indicated above is appropriate.

Robert A. Davis, Edith Cowan University.

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Eddie J. B. van Etten, Edith Cowan University.

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Date: 28/4/15

Appendix A

RE: A continental-scale analysis of feral cat diet in Australia
To Whom It May Concern,

I, Tim S. Doherty, made the following contributions to the paper entitled 'A continental-scale analysis of feral cat diet in Australia': conceived the original idea, collated the datasets, performed most of the analyses, wrote the first draft, and led the writing and editing of the final manuscript.

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Appendix D

RE: Response of feral cats to a track-based baiting programme using *Eradicat*® baits

To Whom It May Concern,

I, Tim S. Doherty, made the following contributions to the paper entitled 'Response of feral cats to a track-based baiting programme using *Eradicat*® baits': conceived the original idea, designed the study, collected and analysed the data, wrote the first draft, and led the writing and editing of the final manuscript.

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Date: 27 April 2015

I, as a co-author, endorse that this level of contribution by the candidate indicated above is appropriate.

Dave Algar, WA Department of Parks and Wildlife.

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Date: 29/4/15

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Chapters 1 & 6


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Perspective

Multiple threats, or multiplying the threats? Interactions between invasive predators and other ecological disturbances

 CrossMark

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ABSTRACT

Invasive species have reshaped the composition of biomes across the globe, and considerable cost is now associated with minimising their ecological, social and economic impacts. Mammalian predators are among the most damaging invaders, having caused numerous species extinctions. Here, we review evidence of interactions between invasive predators and six key threats that together have strong potential to influence both the impacts of the predators, and their management. We show that impacts of invasive predators can be classified as either functional or numerical, and that they interact with other threats through both habitat- and community-mediated pathways. Ecosystem context and invasive predator identity are central in shaping variability in these relationships and their outcomes. Greater recognition of the ecological complexities between major processes that threaten biodiversity, including changing spatial and temporal relationships among species, is required to both advance ecological theory and improve conservation actions and outcomes. We discuss how novel approaches to conservation management can be used to address interactions between threatening processes and ameliorate invasive predator impacts.

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Contents

1. Introduction	61
1.1. Interactions between threats	61
2. Key threats that interact with invasive predators	62
2.1. Habitat-mediated threats	62
2.1.1. Land clearing	62
2.1.2. Altered fire regimes	63
2.1.3. Grazing by large herbivores	63
2.2. Community-mediated threats	64
2.2.1. Top-predator declines	64
2.2.2. Altered prey populations	64
2.2.3. Anthropogenic resource subsidies	64
3. Synthesis and applications	64
3.1. Maintaining habitat complexity	65
3.2. Re- not de-wilding	65
3.3. Management of resource subsidies	65
3.4. Integrated multi-species pest management	65
3.5. Conclusions	66
Role of the funding source	66

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A critical review of habitat use by feral cats and key directions for future research and management

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Abstract. Feral cats (*Felis catus*) have a wide global distribution and cause significant damage to native fauna. Reducing their impacts requires an understanding of how they use habitat and which parts of the landscape should be the focus of management. We reviewed 27 experimental and observational studies conducted around the world over the last 35 years that aimed to examine habitat use by feral and unowned cats. Our aims were to: (1) summarise the current body of literature on habitat use by feral and unowned cats in the context of applicable ecological theory (i.e. habitat selection, foraging theory); (2) develop testable hypotheses to help fill important knowledge gaps in the current body of knowledge on this topic; and (3) build a conceptual framework that will guide the activities of researchers and managers in reducing feral cat impacts. We found that feral cats exploit a diverse range of habitats including arid deserts, shrublands and grasslands, fragmented agricultural landscapes, urban areas, glacial valleys, equatorial to sub-Antarctic islands and a range of forest and woodland types. Factors invoked to explain habitat use by cats included prey availability, predation/competition, shelter availability and human resource subsidies, but the strength of evidence used to support these assertions was low, with most studies being observational or correlative. We therefore provide a list of key directions that will assist conservation managers and researchers in better understanding and ameliorating the impact of feral cats at a scale appropriate for useful management and research. Future studies will benefit from employing an experimental approach and collecting data on the relative abundance and activity of prey and other predators. This might include landscape-scale experiments where the densities of predators, prey or competitors are manipulated and then the response in cat habitat use is measured. Effective management of feral cat populations could target high-use areas, such as linear features and structurally complex habitat. Since our review shows often-divergent outcomes in the use of the same habitat components and vegetation types worldwide, local knowledge and active monitoring of management actions is essential when deciding on control programs.

Additional keywords: *Felis catus*, habitat selection, home range, introduced predator, invasive predator, predator control.

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Introduction

Invasive mammalian predators have caused or contributed to the decline and extinction of many species worldwide (Salo *et al.* 2007). Examples include the red fox (*Vulpes vulpes*) (Johnson 2006), mustelids (Mustelidae) (King and Moody 1982; Salo *et al.* 2010), rats (*Rattus* spp.) (Jones *et al.* 2008; Capizzi *et al.* 2014) and the domestic cat (*Felis catus*) (Medina *et al.* 2011; Duffy and Capece 2012). Humans have introduced the domestic cat to almost every region of the world and self-sustaining wild populations now exist in a wide variety of landscape types including deserts, forests and tropical to sub-Antarctic islands (Long 2003). Animals in these populations are generally termed 'feral', meaning that they are descended from domesticated ancestors but now exist in a free-living state with no direct dependence on humans. Feral cats are distinguished from 'unowned' cats (stray or semiferal) in that unowned cats

remain dependent on humans for at least the incidental provision of resources such as food or shelter.

Feral cats are almost exclusively carnivorous and generally obtain most of their food resources by hunting live prey (Fitzgerald and Turner 2000). Feral cats are acknowledged as one of the world's worst 100 invasive species (Lowe *et al.* 2000) and are thought to have been an important contributing factor to at least 14% of bird, reptile and mammal extinctions globally (Medina *et al.* 2011) and at least 16 mammal extinctions in Australia (Johnson 2006). Predation by feral cats can jeopardise conservation programs aiming to reintroduce native fauna into areas of their former range (Moseby *et al.* 2011; Potts *et al.* 2012), and cats can have non-lethal impacts on susceptible populations through competition, disease transmission, induced predator-avoidance behaviour and hybridisation (Daniels *et al.* 2001; Medina *et al.* 2014). Reducing the impacts of feral cats

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Dietary overlap between sympatric dingoes and feral cats at a semiarid rangeland site in Western Australia

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Abstract. The diet of sympatric dingoes and feral cats was studied in the semiarid southern rangelands of Western Australia. A total of 163 scats were collected over a period of 19 months. Rabbit remains were the most common food item in cat scats, followed by reptiles, small mammals and birds. Macropod remains were the most common food item in dingo scats, followed by rabbits and birds. Dingo scats did not contain small mammal remains, and infrequently contained arthropod and reptile remains. Cat and dingo scats contained remains from 11 and six mammal species, respectively. Of the small mammals, cat scats contained rodent remains more frequently than those of dasyurids. Dietary diversity of cats was higher than for dingoes and dietary overlap between the two species was relatively low.

Additional keywords: *Canis lupus dingo*, diet, *Felis catus*, prey.

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Introduction

Humans have introduced the domestic cat (*Felis catus*) to almost every region of the world (Long 2003). Cats live with humans as companion animals and also in self-sustaining feral populations that obtain their food and shelter needs independently of humans (Turner and Bateson 2013). The feral cat is an opportunistic, generalist carnivore; small and medium-sized mammals, such as rodents and rabbits (*Oryctolagus cuniculus*), are their primary food source in many locations, but they also feed on birds, reptiles, amphibians, invertebrates and carrion to varying degrees (Fitzgerald and Turner 2000; Doherty *et al.* 2015a).

Feral cats and red foxes (*Vulpes vulpes*) were introduced to Australia by Europeans and have contributed to the extinction of more than 20 mammal species and the decline of many other taxa (Dickman 1996; Woinarski *et al.* 2014). Rabbits and rodents are the staple prey of feral cats in Australia, but they feed on a total of 400 vertebrate species, including 16 globally threatened taxa (Doherty *et al.* 2015a). Doherty *et al.* (2015a) found that the diet of feral cats in Australia varies across biogeographical gradients, with reptiles being consumed most frequently in arid areas, medium-sized mammals most in the south-east and rodents the most in the north. A negative relationship was found between cat consumption of small mammals and rabbits, i.e. where cats ate less rabbits, they ate more small rodents and dasyurids (Doherty *et al.* 2015a). These patterns illustrate that local knowledge is essential to understanding the diet of feral cats and hence informing management action.

Cats are sympatric with foxes and dingoes (*Canis lupus dingo*) in many parts of Australia and there is a growing body of knowledge indicating that these larger predators can have temporally and spatially suppressive effects on feral cats

(Molsher 1999; Brawata and Neeman 2011; Brook *et al.* 2012; Krauze-Gryz *et al.* 2012; Marlow *et al.* 2015). Other studies have recorded nil or positive relationships between cats and dingoes (reviewed in Allen *et al.* 2015), which is to be expected given the wide distribution over which the two species co-occur. Dingoes have the largest body size of the three species and cats the smallest (Van Dyck *et al.* 2013). Accordingly, their prey sizes scale proportionally with body size, i.e. dingoes consume the largest prey and cats the smallest, although the three species do show varying degrees of dietary overlap (Paltridge 2002; Glen *et al.* 2011). In eastern Australia, Glen *et al.* (2011) found that cats and foxes had the highest degree of overlap, and cats and wild dogs (*Canis lupus dingo*, *C. lupus familiaris* and their hybrids) the least. High levels of dietary overlap between sympatric carnivores may indicate resource competition, which can lead to aggression between species, including intraguild predation (Polis *et al.* 1989; Donadio and Buskirk 2006). Alternatively, competition may not exist if the prey base is large enough to be shared between the two predators (Polis *et al.* 1989). Documenting the degree of dietary overlap is a useful first step in determining whether resource competition may exist between sympatric carnivores.

The aim of this study was to describe and quantify the diet of sympatric feral cats, foxes and dingoes in the southern rangelands of Western Australia. I sought to: (1) identify what species of fauna the three carnivores prey on, (2) determine the relative contribution of different food groups to their diet, and (3) examine the degree of dietary overlap between the three species. I discuss the findings in the context of previous dietary studies from Australia. Relatively small sample sizes meant that it was not possible to make seasonal comparisons of predator diets. Also, lack of data on the availability of all prey groups meant that

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Chapter 4

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Response of a shrubland mammal and reptile community to a history of landscape-scale wildfire

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Abstract. Fire plays a strong role in structuring fauna communities and the habitat available to them in fire-prone regions. Human-mediated increases in fire frequency and intensity threaten many animal species and understanding how these species respond to fire history and its associated effect on vegetation is essential to effective biodiversity management. We used a shrubland mammal and reptile community in semiarid south-western Australia as a model to investigate interactions between fire history, habitat structure and fauna habitat use. Of the 15 species analysed, five were most abundant in recently burnt habitat (8–13 years since last fire), four were most abundant in long unburnt areas (25–50 years) and six showed no response to fire history. Fauna responses to fire history were divergent both within and across taxonomic groups. Fire management that homogenises large areas of habitat through either fire exclusion or frequent burning may threaten species due to these diverse requirements, so careful management of fire may be needed to maximise habitat suitability across the landscape. When establishing fire management plans, we recommend that land managers exercise caution in adopting species-specific information from different locations and broad vegetation types. Information on animal responses to fire is best gained through experimental and adaptive management approaches at the local level.

Additional keywords: Australia, fire management, lizard, prescribed fire, rodent, wildfire.

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Introduction

Wildfire plays an important role in structuring plant and animal communities in fire-prone regions (Whelan *et al.* 2002). Many species tend to show a strong response to fire and a large number of studies can be found that show either positive (Ashton *et al.* 2008; Conway *et al.* 2010; Rogers *et al.* 2013; Venne and Frederick 2013), negative (Baker *et al.* 2010; Horn *et al.* 2012) or mixed effects (Briani *et al.* 2004; Ukmar *et al.* 2007; Valentine *et al.* 2012; Albanesi *et al.* 2014) of fire on the occurrence, abundance and richness of a suite of vertebrate taxa. The diversity of responses is a product of the life history, dispersal capacity and autecology of the species involved, as well as the effects of fire on habitat through changes in food and shelter availability (Whelan *et al.* 2002). Species within broad taxonomic groups do not necessarily respond to fire in the same way, so reconciling the competing needs of different species can be difficult. Recent attempts to do so for birds in fire-prone Mediterranean landscapes have demonstrated the need to consider species autecology and habitat preferences in conservation

planning (Vallecillo *et al.* 2013). The state of knowledge, however, remains poor for many taxa, especially reptiles and small mammals, and for many habitats, including non-forest habitats such as shrublands.

The immediate effect of fire on fauna includes animal mortality and in the weeks following a fire, surviving animals may increase their movement in search of new shelter, or disperse to more suitable habitat (Legge *et al.* 2008; Driscoll *et al.* 2012). As vegetation recovers over the longer term, changes in the availability of key resources like food (Vernes *et al.* 2004), nesting sites (Kern *et al.* 2012) and woody debris (Haney *et al.* 2008) alter fauna habitat suitability and hence cause successional changes in fauna communities. For example, vegetation cover, which generally increases with time since fire, influences thermoregulatory opportunities for reptiles, so distinct species assemblages are often suited to either early or late post-fire habitats (Daly *et al.* 2008; Santos and Cheylan 2013). Vegetation cover also provides protection from predators (Sutherland and Dickman 1999) and post-fire successional

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Chapter 5



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A game of cat-and-mouse: microhabitat influences rodent foraging in recently burnt but not long unburnt shrublands

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We investigated the influence of vegetation structure and fire history on the foraging behavior of small rodents (*Notomys mitchellii*, *Pseudomys hermannsburgensis*, and *Mus musculus*) by conducting giving-up density (GUD) experiments in recently burnt (9–13 years since last fire) and long unburnt shrublands (> 40 years), and open and sheltered microhabitats, in a semiarid region of Western Australia. We predicted that rodents would spend less time foraging in recently burnt shrublands and open microhabitat and that the influence of microhabitat would be weaker in long unburnt compared to more recently burnt vegetation. Our findings show that fire history and microhabitat structure influence the foraging behavior of the study species and that the influence of microhabitat varies between fire histories. GUDs were higher in long unburnt vegetation and in open microhabitats. There was a microhabitat effect in recently burnt vegetation, but not in long unburnt. Rodents foraged more in sheltered microhabitats probably because predator encounters are less likely to occur there and it provides them with greater refuge from predation. The presence of a microhabitat effect in recently burnt, but not long unburnt vegetation suggests that understory vegetation density is more important in mediating predation risk than canopy density. Future studies of small mammal responses to land management actions should include behavioral, as well as population-level responses to differing fire regimes.

Key words: Australia, feral cat, fire, foraging behavior, giving-up density, *Notomys*, predation risk, *Pseudomys*, rodent

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Vegetation cover provides small mammals with food, shelter, nesting sites, and refuge from predators (Sutherland and Dickman 1999; Monamy and Fox 2000). Small mammals assess predation risk using indirect cues and minimize predator encounters by modifying their activity (Rosenzweig 1981; Lima and Dill 1990). Habitat structure is a well-studied cue and can indicate relative predation risk if prey vulnerability depends upon vegetation structure (Verdolin 2006). Encounters with predators are more likely to occur in open areas (Kotler et al. 1988; Dickman et al. 1991; Janssen et al. 2007) and vegetation cover plays an important role in mediating the lethal and nonlethal effects of predation on small mammals (Arthur et al. 2005; Conner et al. 2011). Structurally complex habitats can reduce predation rates by providing refuges for prey (Kotler et al. 1991). For example, in high refuge areas the survival rates and population density of house mice *Mus musculus* were higher than in low refuge areas (Arthur et al. 2005) and preferential use of complex microhabitats during times of high predator activity has been demonstrated for house mice (Dickman 1992), gerbils *Gerbillus* spp. (Abramsky et al. 1996), and Australian desert rodents (Dickman et al. 2010). In addition to changes in predator activity, temporal changes in cover

availability can influence predation risk and subsequently alter the behavior, demographics, and growth rates of prey populations (Arthur et al. 2004; Spencer et al. 2005).

Small mammals are also affected by wildfire and prescribed burning because fire alters vegetation structure and reduces cover availability (Capitaino and Carcaillet 2008; Craig et al. 2010), which can lead to changes in small mammal community composition, particularly in fire-prone regions (Friend 1993; Fontaine and Kennedy 2012; Doherty et al. 2015). Torre and Díaz (2004) found that small mammal abundance and richness decreased with time since fire in Mediterranean forests, whereas Horn et al. (2012) found that recently burnt areas had lower small mammal abundance and richness when compared to unburnt areas in the Mojave Desert, United States. Fire can also affect the dynamics and behavior of small mammal populations, leading to reduced population size, resource availability, and individual fitness, along with increased competition (Sutherland and Dickman 1999).

The influence of vegetation cover and fire on small mammals may have a synergistic influence on predation pressure (Arthur et al. 2010; Conner et al. 2011) because reduced cover caused by fire results in less shelter for prey species and allows

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ORIGINAL
ARTICLE

A continental-scale analysis of feral cat diet in Australia

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ABSTRACT

Aim Reducing the impacts of feral cats (*Felis catus*) is a priority for conservation managers across the globe, and success in achieving this aim requires a detailed understanding of the species' ecology across a broad spectrum of climatic and environmental conditions. We reviewed the diet of the feral cat across Australia and on Australian territorial islands, seeking to identify biogeographical patterns in dietary composition and diversity, and use the results to consider how feral cats may best be managed.

Location Australia and its territorial islands.

Methods Using 49 published and unpublished data sets, we modelled trophic diversity and the consumption of eight food groups against latitude, longitude, mean temperature, precipitation, environmental productivity and climate-habitat regions.

Results We recorded 400 vertebrate species that feral cats feed on or kill in Australia, including 28 IUCN Red List species. We found evidence of continental-scale prey-switching from rabbits to small mammals, previously recorded only at the local scale. The consumption of arthropods, reptiles, rabbits, rodents and medium-sized native mammals varied with different combinations of latitude, longitude, mean annual precipitation, temperature and environmental productivity. The frequency of rodents and dasyurids in cats' diets increased as rabbit consumption decreased.

Main conclusions The feral cat is an opportunistic, generalist carnivore that consumes a diverse suite of vertebrate prey across Australia. It uses a facultative feeding strategy, feeding mainly on rabbits when they are available, but switching to other food groups when they are not. Control programmes aimed at culling rabbits could potentially decrease the availability of a preferred food source for cats and then lead to greater predation pressure on native mammals. The interplay between cat diet and prey species diversity at a continental scale is complex, and thus cat management is likely to be necessary and most effective at the local landscape level.

Keywords

Australia, biogeographical patterns, conservation biogeography, critical weight range, diet, feeding habits, *Felis catus*, feral cat, invasive predator, predation.

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INTRODUCTION

Invasive mammalian predators are a global threat to biodiversity (Salo *et al.*, 2007). Species like the red fox, *Vulpes vulpes* (Johnson, 2006), some rats, *Rattus* spp. (Jones *et al.*, 2008; Capizzi *et al.*, 2014), and the domestic cat, *Felis catus*

(Dickman, 1996; Medina *et al.*, 2011; Duffy & Capece, 2012), have caused numerous declines and extinctions of native species worldwide. The domestic cat is a medium-sized carnivore occupying a range of habitats across a broad global distribution (Turner & Bateson, 2000). Humans keep cats as companion animals, but cats also live in self-sustaining feral

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Response of feral cats to a track-based baiting programme using *Eradicat*[®] baits

By Tim S. Doherty and Dave Algar

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Summary The feral Cat (*Felis catus*) is a significant threat to Australian fauna, and reducing their impacts is considered an essential action for threatened species conservation. Poison baiting is increasingly being used for the broad scale control of feral cats. In this study, we measured the population response of feral cats to a track-based baiting programme using *Eradicat*[®] baits in the semi-arid northern wheatbelt region of Western Australia. Over two years, 1500 baits were laid once annually and the response of feral cats was measured using remote cameras in a before–after, control–impact design. There was a significant reduction in feral cat activity in the second year, but not the first. During bait uptake trials, corvids removed the most number of baits, followed by cats and varanids. The lack of a response to baiting in the first year may be due to existing low cat numbers in the baited area and/or the timing of the baiting. We provide a list of key recommendations to help inform future cat baiting programmes and research.

Key words: 1080, bait, control, *Felis catus*, feral cat, sodium monofluoroacetate.

Introduction

The feral Cat (*Felis catus*) preys on native fauna and is responsible for numerous extinctions globally (Medina *et al.* 2011; Doherty *et al.* 2015b; Woinarski *et al.* 2015). Predation by feral cats can jeopardise conservation programmes aiming to reintroduce native fauna into areas of their former range (Moseby *et al.* 2011b; Potts *et al.* 2012), and cats can have nonlethal impacts on susceptible populations through competition, disease transmission, induced predator avoidance behaviour and hybridisation (Daniels *et al.* 2001; Fancourt & Jackson 2014; Medina *et al.* 2014; Doherty *et al.* 2015a). Cats have been particularly damaging to Australian wildlife and, together with the introduced European Red Fox (*Vulpes vulpes*), have contributed to the extinction of 22 Australian mammals since European settlement (Johnson 2006; Woinarski *et al.* 2015). Cats are considered to be a contributing factor to recent declines in northern Australia's mammal fauna (Fisher *et al.* 2014a; Woinarski *et al.* 2015; Ziembicki *et al.* 2015) and are listed as a *Key Threatening Process* under the Commonwealth *Environment Protection and Biodiversity Conservation Act 1999* (Department of the Environment Water Heritage & the Arts

2008). Reducing their impact is considered an essential action for the conservation of Australian birds and mammals (Denny & Dickman 2010; Garnett *et al.* 2013; Woinarski *et al.* 2015).

Techniques for controlling populations of feral cats include shooting, trapping, poison baiting and exclusion fencing (Denny & Dickman 2010). Cats have successfully been eradicated from a number of islands (DIISE 2014) and fenced mainland reserves using different combinations of control methods. Unfenced mainland sites, on the other hand, require sustained control efforts because cats have a high reproductive output and an aptitude for reinvasion (Read & Bowen 2001; Short & Turner 2005). Both trapping and shooting are time- and labour-intensive methods of pest control, whereas baiting is comparatively more cost-effective when targeting larger areas (Fisher *et al.* 2014b). However, poison baiting of feral cats is notoriously challenging. While the Red Fox, Dingo (*Canis dingo*) and Dingo/Dog (*Canis lupus familiaris*) hybrids ('wild dogs' hereafter) will readily take carrion, inclusive of poison meat baits, inanimate baits are assumed to be less preferred food items relative to normal live prey for feral cats (Fisher *et al.* 2014b). However, feral cats are adaptable enough to scavenge, so where possible

baiting should be timed to coincide with low availability of natural prey resources (Short *et al.* 1997; Algar *et al.* 2007; Moseby & Hill 2011; Christensen *et al.* 2013). Risbey *et al.* (1997) found that four different bait mediums (dried meat baits, a fish-meal-based bait, a bait coated in a flavour enhancer and baited European Rabbit [*Oryctolagus cuniculus*] carcasses) were all ineffective in controlling feral cats at Shark Bay in Western Australia. Other studies also found that dried meat baits were ineffective in controlling cats in arid and semi-arid Western Australia (Burrows *et al.* 2003; Algar & Burrows 2004). However, using fresh meat baits, Burrows *et al.* (2003) were able to reduce cat abundance in Western Australia's Gibson Desert by 75% and 100% during two years of below average rainfall.

The Western Australian Department of Parks and Wildlife (and its predecessors) has developed a bait medium and baiting technique that can effectively reduce feral cat populations, as well as fox and wild dog populations. The bait (*Eradicat*[®]) is similar to a chipolata sausage and is composed of 70% kangaroo meat mince, 20% chicken fat and 10% digest and flavour enhancers (Algar *et al.* 2007, 2013). It weighs ~20 g wet weight, is dried to 15 g, blanched and then frozen (Algar

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